Cryptospores and cryptophytes reveal hidden diversity in early land floras

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Summary

Cryptospores, recovered from Ordovician through Devonian rocks, differ from trilete spores in possessing distinctive configurations (i.e., hilate monads, dyads, permanent tetrads). Their affinities are contentious, but knowledge of their relationships is essential to understanding the nature of the earliest land flora. This review brings together evidence about the source plants, mostly obtained from spores extracted from minute, fragmented, yet exceptional anatomically preserved fossils. We coin the term cryptophytes for plants that produced the cryptospores and show them to have been simple terrestrial organisms of short stature (i.e. millimetres high). Two lineages are currently recognised. *Partitatheca* shows a combination of characters (e.g., sporophyte bifurcation; stomata, dyads) unknown in plants today. *Lenticulatheca* encompasses discoidal sporangia containing monads formed from dyads with ultrastructure closer to higher plants as exemplified by *Cooksonia*. Other emerging groupings are less well characterised, and their precise affinities to living clades remain unclear. Some may be stem group embryophytes or tracheophytes. Others are more closely related to the bryophytes, but they are not bryophytes as defined by extant representatives. Cryptophytes encompasses a pool of diversity from which modern bryophytes and vascular plants emerged, but were competitively replaced by early tracheophytes. Sporogenesis always produced either dyads or tetrads indicating strict genetic control. The long held consensus that tetrads were the archetypal condition in land plants is challenged.

I. Introduction

Over the past 50 years, the discovery and analysis of fossil spore assemblages dispersed in rocks of lower Palaeozoic age (470 – 419.2 million years) has revolutionised our understanding of the colonization of the land by plants. Although there were some pre-1960s

pioneers (e.g. Lang, 1925; Thomson, 1940; Eisenack, 1944; Naumova, 1953; Radforth & McGregor, 1954; Chibrikova, 1959), the application of palynological methods developed from the 1960s such that it opened up a new window on to early floras (e.g. McGregor, 1960, 1961; Chaloner, 1963; Streel, 1964; Allen, 1965; Richardson, 1960, 1962, 1965, 1967; Richardson & Lister, 1969; Richardson & Ioannides, 1973). Prior to this, research focused on macroscopic remains (i.e., plant leaves, stems, wood, seeds, etc.) from the Devonian Period, which yielded a record of early vascular plants that was both diverse and rich in detail (e.g. Kräusel & Weyland, 1935; Lang, 1937; Høeg, 1942; Chaloner, 1970). This megafossil record formed the foundation of our understanding of the nature of early land floras, and it defined the temporal framework for investigating evolutionary trends and their broader effects on Earth Systems (Banks, 1968; Banks, 1970; Chaloner, 1970; Niklas *et al.*, 1985). Palynology extended significantly the stratigraphic and geographic scope of enquiry, and it brought to light a hidden diversity of enigmatic plants. Key early studies showed that plant life on land extended much further back stratigraphically than did the macrofossil remains (reviewed by Gray, 1985; Richardson, 1985; Richardson & McGregor, 1986), but precisely how far is debated both in terms of evidence acceptable to palynologists (Richardson, 1988, 1992; Steemans, 2000; Wellman & Gray, 2000; Taylor & Strother, 2008; Taylor & Strother, 2009; Steemans *et al.*, 2010; Wellman, 2010; Strother *et al.*, 2011) and the fit to calibrated molecular phylogenies (Clarke *et al.*, 2011; Kenrick, 2011; Magallón *et al.*, 2013; Rota-Stabelli *et al.*, 2013). Also revealed was an unanticipated diversity of palynomorphs, some of which are uncontroversially attributable to land plants (e.g., trilete monads also known as trilete spores; Steemans *et al.*, 2009), whereas the affinities of others (e.g., obligate tetrads, dyads, alete monads also known as cryptospores) are less clear (Rubinstein *et al.*, 2010; Steemans *et al.*, 2010; Wellman, 2010; Strother *et al.*, 2011) (Fig. 1). Recently, there has also been a shift in thinking about the geographic region of origin of land plants from Laurussia to

Gondwana, based on evidence from palynomorphs (Steemans *et al.*, 2010). These discoveries raise two related questions. First, why does the stratigraphic record of palynomorphs precede to such a great extent the record of macroscopic plant remains? Second, what sort of plants produced the cryptospores, and how are they related to living species? The answer to the first question lies partly in the nature of the rock record during the early part of the Palaeozoic Era, where significant changes in the proportions of terrestrial and marine rocks are thought to effectively open and close taphonomic windows on to macrofossil and palynomorph evidence (Kenrick *et al*., 2012) and partly because of changes in preservation potential of the plants themselves. Progress in addressing the second question has relied on the comparative study of spore wall ultrastructure. The application of transmission electron microscopy to both living and fossil palynomorphs has been critical to identifying features linking some cryptospores to basal living groups of embryophytes (Taylor, 1995a; Taylor, 1995b; Taylor, 1996; Taylor, 1997). At the same time, the discovery of minute, fragmentary, but remarkably well-preserved fossil plants at several sites in the Welsh Basin has furnished direct evidence of the plants that produced the cryptospores (Edwards *et al.*, 1995a; Edwards *et al.*, 1996; Wellman *et al.*, 1998a; Wellman *et al.*, 1998b; Edwards *et al.*, 1999; Wellman, 1999). We review the nature of this fossil evidence, and we explore its implications for our understanding of early land floras, the organisms they contained and their relations to living plants.

II. History, characters and disparity in cryptospores

Dispersed palynomorphs can be linked to their source plants through comparative morphology with varying degrees of confidence. One of the common characters of early vascular plant fossils is the trilete monad, which is a spore with a sporopollenin-rich wall that formed in a sporangium as a product of meiosis. This spore type is commonly found *in situ* in

megafossils of the Devonian Period (Allen, 1980; Gensel, 1980), but in its dispersed form it is present in Lower Silurian palynomorph assemblages (Gray 1985), significantly predating the oldest unequivocal macrofossil record of vascular plants. This early record of trilete spores, which now extends into the Upper Ordovician (Mid Katian: Caradoc - Ashgill) (Steemans *et al*., 2009, Saudi Arabia), is widely regarded as a benchmark for the origin of vascular plants, but this interpretation is clouded by the fact that trilete monads are also known to be characteristic of some living bryophytes (Table 1). It is conceivable therefore that the early trilete monads might represent a broader grouping within basal embryophytes.

As the early Palaeozoic record of trilete spores came under scrutiny, it became apparent that other distinctive palynomorphs formed a significant component of non-marine assemblages (e.g. Gray & Boucot, 1971, 1972; Richardson & Ioannides, 1973; Gray *et al*., 1974; Pratt *et al*., 1978; Strother & Traverse, 1979; Miller & Eames, 1982). These took the form of alete monads and other types that were dispersed as tetrads and dyads, some of which were enveloped in a second wall layer. Although the affinities of these palynomorphs could not easily be established, these discoveries heralded a breakthrough towards the understanding of a new facet of early land vegetation. Permanent tetrahedral tetrads were first recognised by Gray & Boucot (1971) from the lower and middle Llandovery (basal Silurian) of western New York State. They initially hypothesised that both permanent tetrads and trilete monads were the products of vascular plants, but they also recognised that a bryophytic origin could not be precluded. In other words, some of the new enigmatic palynomorphs were probably derived from land plants and possibly from bryophyte-like organisms, hinting at a greater diversity of plants (Fig. 1).

Recognition of these diverse palynomorphs as a separate group began to be formalised when Strother & Traverse (1979) provided generic names and diagnoses for the permanent tetrads (including *Tetrahedraletes*) and dyads (*Dyadospora*), based on an assemblage from

the Llandovery and Wenlock of Pennsylvania. Building on this, Richardson *et al*. (1984) erected the informal category (Anteturma) *Cryptosporites*, also known as cryptospores, with the following definition: *'non-marine sporomorphs, with no visible haptotypic features such as contact areas or tetrad marks. Single grains or monads, 'permanent' dyads and tetrads are included'* (Richardson *et al*., 1984, p. 116). The prefix 'crypto' referred to their unfamiliar configurations and absence of knowledge regarding their producers and affinity. In 1988, he emended his definition to include the separated products of dyads (i.e., hilate monads: monads with a large circular contact area) (Richardson, 1988). Other usages range from the very general, e.g. Strother & Beck (2000) who regarded cryptospores as a class of organic walled microfossils produced by terrestrial plants (a sub-aerial equivalent of acritarchs), to formal definitions that seek to eliminate some ambiguities and possible confusions with acritarchs and which also introduce specific notions of affinity with embryophytes (e.g., Steemans, 2000). In this review we adhere to the definition of Richardson (1988), because it is based on straightforward morphological criteria that can be used to recognise a cryptospore and it does allude to affinities with specific plant groups. We concentrate on two cryptospore groups based on their configurations, either as tetrahedral tetrads or dyads. Tetrads are always permanent (also known as obligate), meaning that they are dispersed as polyads, whereas dyads are dispersed either as polyads or as monads. In contrast to trilete spores, such monads are alete and possess an extensive proximal contact feature termed a hilum. The entire permanent polyad of both tetrads and dyads can be surrounded by an envelope, which may be loose or so closely adherent that it is difficult to distinguish. The surface of the envelope may be sculptured, while that of the enclosed polyad is usually smooth (e.g. *Velatitetras* Burgess, 1991). Naked polyads (i.e. those lacking an envelope), may have smooth or sculptured surfaces, and the latter is more common in younger Upper Silurian to Lower Devonian rocks.

The sculpture on cryptospores provides an additional suite of characters that enable species to be distinguished. These cryptospores species are regarded as a proxy for species diversity (disparity) in the source vegetation. Detection of disparity through the analysis of palynomorphs with very simple morphology, as exemplified by the smooth (naked) polyads, presents far greater challenges, although recent studies involving thin sections and TEM indicate far greater variation in wall characters in dispersed and *in situ* permanent cryptospores than previously recorded by SEM and light microscopy (Taylor, 1995b, 2002; Edwards *et al*., 1999; Edwards *et al*., 2012b) (Fig. 2).

In initial attempts to increase the number of distinguishing characters in cryptospores, Wellman & Richardson (1993) introduced the terms fused and unfused to differentiate between tetrads and dyads which had superficial 'lines of attachment' / sutures between tetrad units (unfused) and those that did not (fused). Thus, for example, the laevigate genus *Tetrahedraletes* Strother & Traverse, 1979 emend. Wellman & Richardson, 1993 is a permanent unfused tetrad, while *Cheilotetras* Wellman & Richardson, 1993 is a laevigate, permanent fused tetrad. However, the ultrastructural basis underpinning this distinction is particularly difficult to elucidate in the absence of thin sections, as later appreciated by Richardson (1996c) and Wellman (1996). This introduces a further taphonomic problem because diagenesis and charring can result in homogenisation of adjacent walls. A further possibility is that the absence of sutures at the junctions between units may reflect the presence of a thin adherent envelope.

By far the most important advance in elucidating the affinities of Ordovician and Silurian dyads was made by Taylor in his TEM work on the wall ultrastructure of *Dyadospora murusdensa* Strother & Traverse, 1979 emend. Burgess & Richardson, 1991 (Taylor, 1995a; 1996, figs. 10-13) and *Dyadospora murusattenuata* Strother & Traverse, 1979 emend. Burgess & Richardson, 1991 (Taylor, 1997, pls. I, II). Variation in ultrastructure was

observed within this genus. Of particular note were the spore walls of *D. murusdensa* and *D. murusattenuata* Type I, their inner layers possessing a laminate construction (Fig. 2a, b). Laminae are distinguished from 'white line centred lamellae', the latter being fine structures (60 – 130 Å) that appear early in spore wall development in extant plants. The latter are subsequently covered on both surfaces by sporopollenin layers and fuse together to form tripartite lamellae (Taylor, 2009). Often, but not always, the tripartite structures are occluded by further sporopollenin deposition, forming laminae (Taylor, 2009). Well preserved stacked laminae were also observed in sections of *in situ* permanent naked dyads from the oldest known spore masses (Late Ordovician; Saudi Arabia) (Wellman *et al*., 2003, fig. 2). By contrast, dispersed Ordovician and Silurian tetrads have homogeneous (Fig. 2f ii) or irregularly or weakly striated walls (Fig. 2f i, iii) (Taylor, 2002), except for a mid-Ordovician example in which a highly convoluted single lamina is internal to a thick homogeneous wall (Taylor, 2009). The wall ultrastructure of the dyads and the tetrahedral configuration of the tetrads have been used to posit an hepatic affinity (e.g. Gray, 1985). We will further explore this hypothesis based on an analysis of cryptospores found *in situ* in cryptophyte fossils.

III: *In situ* cryptospores

1. Introduction

This review is based on very small, almost all charcoalified, fossils (termed mesofossils) comprising the fertile tips of small plants. They come from two localities in Shropshire, U.K. The older assemblage is found in the Downton Castle Formation exposed in a small cliff at the junction of Ludford Lane and Leominster Road, Ludlow, in strata dated as Přídolí (Late Silurian; ~419Ma) on the presence of dispersed spores of the *tripapillatus –spicula* Sporomorph Assemblage Biozone (Richardson & McGregor, 1986). The younger occurs in a stream section to the north side of Brown Clee Hill, belonging to the lower part of the Ditton

Group, deposited about four million years later (Edwards & Richardson, 2004). Spores indicate the horizon belongs to the middle subzone of the *micrornatus – newportensis* Sporomorph Assemblage Biozone, indicating an early Lochkovian (Lower Devonian) age (Richardson & McGregor, 1986). The quality and extent of preservation (subtending axes are very rare) is such that the diagnoses and characterization of each group described here are based on a concatenation of evidence. However, there is often a consistent association of cryptospore type with sporangial morphology, as summarised below in A-D, allowing the distinction of lineages and insights into the diversity and affinities in early land vegetation. The *in situ* spores can then be related to those in the dispersed spore assemblage from the locality, sometimes even to varietal level, although it is now evident that species in the same dispersed genus may belong to different lineages. For example, the dispersed spore genus *Cymbohilates* Richardson, 1996a, encompasses two groups; hilate monads (e.g. *C. allenii* var. *magnus*, *C. variabilis*), the separation products of dyads, which retain an intact hilum, are found within discoidal sporangia (Morris et al., 2011), and alete monads (namely *C. horridus* complex and *C. cymosus*), produced by the tearing apart of permanent dyads and sometimes possessing partial fragmentary 'hilate apertures' found within valvate sporangia (Edwards et al., 2012a).

2. Descriptions of major groups of sporangia containing cryptospores

A. Permanent polyads in valvate sporangia

(i) Quadrivalvate sporangia (Fig. 3)

(ii) Bivalved elongate sporangia (Fig. 4)

B. Dyads and tetrads in discoidal sporangia

(i) Hilate monads and separating dyads in discoidal sporangia (Fig. 5)

(ii) Permanent sculptured tetrads in discoidal sporangia (Fig. 6)

C. Permanent polyads in sporangia with unknown dehiscence

i) Laevigate permanent dyads (Fig. 4)

ii) Permanent tetrads in bifurcating specimens (Fig. 7)

iii) Permanent enveloped tetrads in spore masses with sporangial coverings (Fig. 7)

D. Alete monads (Fig. 6)

A. *i) Permanent polyads in quadrivalvate sporangia (Fig. 3)*

Distinguishing characters of this group include:

- Sporangial dehiscence into four valves along entire length;
- Sporangial wall comprising at least one layer of large cells;
- Permanent laevigate and sculptured dyads and tetrads;
- Exospore with complex ultrastructure*;
- Occasional stomata on sporangia and subtending axes*;
- Bifurcating axes*.

(*) Rare occurrences.

The genus *Partitatheca* Edwards *et al*. (2012a) was initially erected for quadrivalvate sporangia (Fig. 3a, i, l; Fig. 4a) with longitudinal files of large cells in their walls and permanent dyads with spinous sculpture (Fig. 3c, d, g, j, k). We would now extend the genus circumscription to include those containing dyads with murornate (Fig. 3m, n) and laevigate walls (Fig. 3q), as well as permanent tetrads (Fig. 4b, c).

Considering those containing sculptured permanent dyads, four species were initially distinguished from Lower Devonian specimens; *P*. *splendida*, *P*. *horrida*, *P*. *densa* and *P*. *cymosa* (Edwards *et al*., 2012a), their names reflecting those of spinose varieties of the dispersed spore *Cymbohilates* complex (Richardson, 1996a) (Fig. 3c, d, i, j). The sporangia of

each species differ in overall morphology (Fig. 3a, i), shape of individual valves, presence or absence of stomata (Fig. 3b) and in one case, possible persistent attachment at the apex (Edwards *et al*., 2012a, fig. 8A). In one case, an incomplete basal portion of a sporangium containing *C. horridus* Richardson, 1996a terminates a branching stem (Fig. 3f, g) with occasional stomata (Habgood, 2000).

Most of the *in situ* spore species have typical spines, variation deriving from the density, degree of fusion and clustering of the spines (Fig. 3c, g). In *C. cymosus* Richardson, 1996a, they are arranged in bizarre star-shaped rosettes of basally fused spines (Fig. 3j, k). *Cymbohilates horridus* var. *splendidus* Richardson in Edwards *et al*., 2012a occurs within the type species, *P. splendida* and possesses pointed spines that cluster into pairs or small groups or are irregularly distributed (Fig. 3c) (Edwards *et al*., 2012a).

Cymbohilates horridus var. *splendidus* shows the most complex ultrastructure recorded to date by TEM in Devonian cryptospores (Fig. 3e). Each spore of the dyad is completely surrounded by a relatively electron-lucent homogenous layer, with darker flecks (possibly representing lamellae) in the mid region, showing complete fusion at the junction marked by a continuous dark line where the proximal surfaces meet (Fig. 2d i). The two fused spores are further enclosed in a complexly layered wall composed of at least five layers. Perhaps the most significant of these is a <40nm zone of alternating dark and light lines (Fig. 2d i; Fig. 3e), interpreted as laminae (*sensu* Taylor, 2009), that is sandwiched between an electron-dense layer that extends into the sculpture and a further narrower internal layer. A sporadically preserved, tightly adhering, outermost electron-lucent layer is also recorded. Spores assigned to *C. horridus sensu lato* within the bases of sporangia attached to a bifurcating axis (Fig. 3f, g) have a similar overall construction, with a tri-layered wall, but have a further well-developed separating external layer (Fig. 3h) (Habgood, 2000). Along

with other specimens of *Cymbohilates* within *Partitatheca*, these spores lack a laminate construction.

The disparity of *in situ* spores within this sporangia type was extended with the discovery of a group of valvate sporangia from the same locality, assigned to *Partitatheca* sp. and cf. *Partitatheca* sp. (Fig. 3l), that contain permanent dyads with murornate sculpture (Fig. 3m, n) (Morris *et al*., 2012a). Such spores are closest to the dispersed spore taxon *Chelinohilates erraticus* Richardson, 1996a. Fortuitous fractures and thin sections indicate a similar overall construction to *C. horridus* var. *splendidus*, the two units fused at their proximal surfaces (Fig. 3n), and completely encompassed by an outer, highly folded wall (Morris *et al.*, 2012a). There is only one example of this group known from the Upper Silurian. It is a disintegrated specimen (NMW97.42G.1) with one intact valve remaining of a presumed quadrivalvate sporangium (Wellman *et al*., 1998a; Fig. 3p). It contains permanent 'unfused' laevigate dyads, belonging to *Dyadospora murusdensa* (Wellman *et al*., 1998a). In section the distal spore walls are bi-layered. The inner layer of each dyad member has a homogeneous structure, apart from a line of voids running close to and parallel with the lumen (Fig. 3r) and is continuous around each dyad member (Wellman *et al*., 1998a). The outer layer encompasses the whole dyad and is variable in thickness, to absent in places. This layer could be a thick envelope or extra-exosporal material (Wellman *et al*., 1998a) or an outer wall similar to that observed in *C. horridus* var. *splendidus* and *Chelinohilates erraticus*. The nature of the junction between proximal surfaces is unknown, although TEM sections show a thickening of the outer layer where the two units of the dyad meet at the surface (Fig. 3r), similar to that observed in *Dyadospora murusattenuata* Type II sectioned by Taylor (1997) (Fig. 2a).

All of the dyads described above were permanent, not only because of the fusion between the proximal surfaces, but also due to an outer encompassing wall. Where these spores occur

as monads in the dispersed record (Richardson, 1996a), they have been torn apart, rather than separating naturally.

Although our original diagnosis of *Partitatheca* stated that the *in situ* spores were dyads (Edwards *et al*., 2012a), more recent work has revealed a single Lochkovian valvate sporangium containing permanent tetrads (Edwards *et al*., 2012b). Specimen NMW2012.17G.3 is a small sporangium similar to *Partitatheca splendida* (Fig. 4a), containing laevigate tetrads with collapsed and heavily folded distal walls (Fig. 4b). These lack 'lines of attachment'/sutures between members of the tetrad, the junctions being marked by furrows (Fig. 4c). Thus they superficially resemble *Cheilotetras* (Edwards *et al*., 2012b). Sections show thin homogeneous to granular spore walls, becoming narrower proximally, where they are fused together (Fig. 4d). A wedge-shaped 'plug' of material occurs at the junction, similar to that observed in *Dyadospora murusdensa* described above (arrow a in Fig. 4d). A thin outer layer encompasses the whole tetrad (arrow b in Fig. 4d).

A. *ii) Permanent tetrads in bivalved elongate sporangia*

Two additional elongate sporangial specimens containing permanent tetrads possess a valvate construction, but are bi-valved rather than quadrivalvate.

Lower Devonian specimen NMW99.11G.2 is an elongate, narrow sporangium composed of two valves that are partially separating, with complete apical rounded tips, but fractured proximally (Fig. 4e). Unlike those in the quadrivalvate sporangia, cell walls are less well defined and smaller, although their topography suggests some degree of lateral shrinkage. Stomata were not observed. The *in situ* spores are laevigate permanent tetrads with collapsed distal walls and no 'lines of attachment/ sutures' (Fig. 4f), but contacts between members of the tetrad are commonly marked by superficial furrows. They are thus most comparable with *Cheilotetras*. In semi-thin section, the spores have a similar organisation as the laevigate

permanent tetrads within the quadrivalvate sporangium (NMW2012.17G.3); thin spore walls, narrowing proximally, where they are fused together, with an outer wall that encompasses the whole spore. However, the TEM sections are different, showing gross layering or laminate structures (Fig. 4g).

The second specimen, NMW99.19G.2, from the same locality was originally described by Habgood (2000). This sporangium consists of two valves, with rounded apical tips, that have separated with the valve margin walls curled inwards (Fig. 4h). The outer surfaces are smooth, apart from where cell outlines are faintly visible (Habgood, 2000, fig. 20). They are comparable in size to those of *Partitatheca*. Stomata were not observed. The nature of the *in situ* spores was difficult to determine in SEM, but their main characteristics are irregular, flexuous muri, forming broad reticula (Fig. 4i) (Habgood, 2000). TEM sections revealed that these spores are envelope-enclosed fused tetrads, and thus belong to the dispersed spore genus *Velatitetras*. Their ultrastructure is quite complex, comprising a thick envelope with voids, which is detached from the inner spore units that have homogeneous walls, but outward projections and occasional voids near the lumina (Figs. 2g ii; 4j).

B. *i) Hilate monads and separating dyads in discoidal sporangia (Fig. 5)*

Laevigate and sculptured hilate monads occur in abundance in Upper Silurian and Lochkovian palynological assemblages in the Welsh Basin, sometimes outnumbering trilete monads in sample counts (e.g. Richardson, 2007), and with an increasing proportion of sculptured forms in the younger rocks. Both forms have been recorded in discoidal spore masses covered by an acellular cuticular layer (Fig. 5a, d) with a central tuft on one surface (Fig. 5e), presumably marking the position of attachment of the subtending axis, although more extensive remains of the latter have never been recorded. In 2011, Morris *et al*. erected

a new genus, *Lenticulatheca,* to accommodate such fossils. Members are united in the possession of:

- discoidal presumed terminal sporangia;
- sporangial wall represented by a laevigate, acellular, cuticular layer;
- sporangial cuticle with white lines, ?lamellae*;
- laevigate and sculptured hilate monads;
- bi-layered exospore/spore wall with variation in relative widths of the layers.

(*) Rare occurrences.

From the Lochkovian assemblage, the presence of sculpture on the distal wall, combined with the nature of the hilum imposes much greater scope for detection of diversity, and allowed Morris *et al*. (2011) to erect four species in their new genus, *Lenticulatheca.* All contained species of the dispersed spore *Cymbohilates,* with one species per sporangium, their names reflecting either distal sculpture or hilate features in the dispersed species. Thus *L. mesodeca* contains spores assignable to *C. mesodecus* Richardson in Morris *et al*., 2011, which are characterized by a smooth hilum and sculpture of equally spaced microgranа (Fig. 5j, k). *L. allenii* contains *C. allenii* Richardson, 1996a, a monad with similarly distributed sculpture of microgranа, microconi, microrugulae and microbaculae, but proximally similar and even smaller sculpture (Fig. 5n, o). In *L. variabilis* spores belong to *C. variabilis* Richardson, 1996a, with regular radial, concentric and tangential folds / muri on the hilum and distal microconi and microbaculae (Fig. 5l, m). *Cymbohilates allenii* var. *magnus* Richardson, 1996a, found in *L. magna*, has an irregular reticulum on the hilum with mainly microgranа on distal and subequatorial surfaces (Fig. 5h, i).

In addition to these, there are also sporangia in coeval and Upper Silurian strata that contain laevigate monads (Fig. 5a, b) (Wellman *et al*., 1998b; = Groups A & E), belonging to the

dispersed spore *Laevolancis divellomedia* (Chibrikova) Burgess & Richardson, 1991 (the authors consider the emendment by Breuer *et al*., 2007 of the younger genus *Gneudnaspora* Balme, 1988 to include the former to be invalid). The Silurian specimens (NMW97.1G.1; NMW96.30G.2, Group A) show two layers, both homogeneous, in TEM (Fig. 5c), with the outer consistently slightly wider (c.10-20%) than the inner. The two Lochkovian specimens (NMW96.30G.4; NMW97.1G.6) have less complete margins (Wellman *et al*., 1998b, fig. 9a, b) and, although placed in the same spore genus as the older ones, their laevigate spores differ in the presence of a low narrow ridge delimiting the hilum (Wellman *et al*., 1998b, fig. 9f, h, j, k). TEM sections show a bi-layered wall (albeit with reversed staining) (Wellman *et al*., 1998b, fig. 9l, n), but the outer layer is much narrower than in the Silurian specimens, their relative dimensions being much closer to those in coeval sculptured forms.

We have no doubt that these specimens belong to the genus *Lenticulatheca* and that two new species should be erected to accommodate the variation in spore characters. Indeed it is obvious from Wellman *et al.* (1998b) where the appellation *Laevolancis divellomedia sensu lato* was employed, that simplicity in spore morphology masks the disparity of the producers as further evidenced by elongate spore masses from the Silurian locality.

B. *(ii) Permanent sculptured tetrads in discoidal sporangia*

The first of two Lower Devonian discoidal sporangia that contain sculptured permanent tetrads is specimen NMW2012.17G.2, which possesses similar sporangial characters as those described above containing hilate monads, with laevigate, acellular cuticular layers representing the sporangial walls (Fig. 6a) (Edwards et al., 2012b). The *in situ* spores are circular and possess ridges and furrows (Fig. 6b, c) that are suggestive of a tetrad configuration. The junctions between the tetrad members are unclear, with no lines of attachment, therefore, apart from occasional splitting (Fig. 6c), the tetrads are interpreted as

permanent. This is also illustrated in thin section, with lack of distinction between the homogeneous distal walls of each tetrad member (Fig. 6d). However, narrow proximal walls are clearly seen extending into the lumen, indicating that, although unfused, the fragility of these walls means it is unlikely that the tetrad would separate successfully. The spores are sculptured with elements ranging from microverrucae, vermiculate/acinoform (biform) coni, with varying degrees of spacing and fusion. They are most similar to the dispersed genus *Acontotetras* Richardson 1996a, but the sculptural elements are too different from the type species (widely spaced grana and microconi), so they were assigned to *Acontotetras* sp. (Edwards *et al.*, 2012b).

The second specimen, NMW2012.17G.1, is a fragment of an originally discoidal sporangium, but unlike the first specimen, possesses a cellular wall (Fig. 6e) (Edwards et al., 2012b). In cross section it comprises a single layer of rectangular cells (Fig. 6f). Degradation of these cells has produced a honeycomb surface pattern, while towards the centre of the specimen a wrinkled surface is suggestive of a cuticular layer (Fig. 6e). Stomata are observed on the proximal surface (Fig. 6e). The sporangium contains permanent sculptured tetrads (Fig. 6g, h), with sculptural elements that range from micrograna, verrucae to biform, with varying degrees of spacing and fusion (Fig. 6i, j). The junctions between tetrad members are unclear under SEM, appearing either as a ridge (Fig. 6i) or a furrow (Fig. 6h), with no clear lines of attachment. Based on surface features alone, these spores were also assigned to the dispersed spore genus *Acontotetras*, specifically the type species *A. inconspicuis* Richardson, 1996a.

In LM thin section and TEM (Fig. 6l, k), the majority of the spore wall is homogeneous, with a thin outer layer that encompasses the entire tetrad, interpreted as an envelope. The distal spore walls are thick, particularly at the junctions between the tetrad members, the latter represented by a sinuous line, accompanied by two narrow tapering walls that extend

freely into the lumen, interpreted as the proximal walls. As with the first specimen, the fragility of these internal walls suggests that the tetrad did not separate naturally, but may have been torn apart.

C. *Permanent polyads in sporangia of unknown dehiscence*

It is important to note here that the following are not considered to be biological groupings but are united by similar characteristics.

i) Laevigate permanent dyads

Two specimens from the Lower Devonian comprise sporangia containing laevigate permanent dyads. The first (NMW96.11G.6) comprises a beaker-shaped sporangium with truncated tip, terminating an unbranched axis lacking anatomy (Fig. 4k), named *Culullitheca richardsonii* Wellman *et al*., 1998a. *In situ* dyads are permanent, but show 'lines of attachment' (Fig. 4l). The spore walls are homogeneous (Fig. 4m). They are similar to *Dyadospora murusdensa*, but their walls are markedly invaginated distally, whereas in the former they are usually inflated.

In the second specimen (NMW97.42G.4), one branch of a bifurcating stem terminates in a fusiform sporangium that tapers distally, named *Fusiformitheca fanningiae* (Fig. 4n; Wellman *et al*., 1998a; Xue & Wang, 2011). The superficial cells of the sporangial wall are large and fusiform, the surface limiting the sporangial cavity minutely reticulate. The dyad walls are thin, highly folded and distally invaginated (Fig. 4o) and covered by a thin, closely adherent envelope. In section the walls are homogeneous (Fig. 4p). As the envelope masks the junction between the dyad members, they could belong to either *Segestrespora laevigata* Burgess, 1991 (an enveloped fused dyad) or *Abditusdyadus laevigatus* Wellman & Richardson, 1996 (an enveloped unfused dyad). It is possible that the sporangium is

immature and intact, and therefore, based on sporangial wall cells, could belong to *Partitatheca*.

ii) Permanent tetrads in bifurcating specimens

Three specimens from the Lower Devonian with either bifurcating sporangia or subtending axes contain permanent tetrads. The first specimen, named *Grisellatheca salopensis* Edwards *et al*., 1999, comprises a short length of smooth axis that terminates in a bifurcating sporangium (Fig. 7a), whose walls are incomplete but show traces of large cells. It contains laevigate fused tetrads with wrinkling across unit junctions suggestive of an envelope and hence affinities with *Velatitetras* (Fig. 7b, c). Where fortuitously fractured, it was observed that the spore walls lacked layering (Fig. 7c).

The second specimen is a bifurcating axis described by Edwards *et al*., 1999 (NMW98.23G.2) (Fig. 7d), in which one branch has a terminal cavity containing laevigate tetrads (Fig. 7e) with minute wrinkles in places and with well defined, slightly sinuous lines of attachment. It is hence attributable to *Tetrahedraletes*. However, the spore wall is bi-layered, with a very narrow electron-dense, sometimes detached, outer layer and a much thicker electron-lucent inner layer surrounding each member of the tetrad (Fig. 7f).

The third specimen (NMW96.11G.3) is a bifurcating axis terminated by the bases of two sporangia or the base of bifurcating sporangium (Edwards *et al*., 1999) (Fig. 7g). Preserved fragments of cells in the sporangium wall are large. The spores are permanent tetrads with an irregular microgranulate sculpture (Fig. 7h), although this sculpture may be a precipitate of tapetal origin, as it is also found on the inside surfaces of the sporangial wall (see page 37 for discussion), and a thick electron-dense envelope that is fused to the spore wall (Fig. 7i). They are most closely attributable to *Velatitetras*. Each unit is surrounded by a three layered wall

comprising a central zone composed of globular material sandwiched between two homogeneous layers.

iii) Permanent tetrads in spore masses with sporangial coverings

Two specimens are united here as discoidal spore masses with sporangial coverings that contain permanent, enveloped tetrads. Spores of NMW96.11G.4 from the Upper Silurian (Edwards *et al*., 1999, mislabelled NMW98.23G.1) are enclosed by an amorphous homogeneous layer (Fig. 7j), but lacks evidence of any axial attachment. The spores are tetrads, enclosed tightly by an adherent envelope, with an irregularly granular outer surface. Sections indicate that the envelope is slightly more electron-dense than the spore wall and limited externally by a darker line (Fig. 7l). The spore wall shows faint striations reminiscent of laminae following surface contours (Fig. 7l). Spores were assigned to *Velatitetras* cf. *anatoliensis* (Fig. 7k) because the envelope sculpture does not exactly match that described for the species (Steemans *et al*., 1996).

The second specimen (V.68196(2)), from the Lower Devonian (Edwards *et al*. 2012b), is an irregularly shaped spore mass partially covered by amorphous ?cuticular material (Fig. 7m). The spores are laevigate tetrads enclosed in envelopes with superficial sinuous folding (Fig. 7n, o). In section this envelope possesses inward projections. The spore walls themselves are homogeneous. Spores were assigned to *Velatitetras* sp. (Edwards *et al*., 2012b).

D. *Alete monads*

A single, poorly preserved specimen of a partial sporangium from the Lower Devonian is included here because it is the only specimen we have found that possesses alete monads (Edwards *et al*., 2012b). The wall comprises two strap-shaped structures with straight, but

incurved, margins (Fig. 6m), suggestive of controlled longitudinal dehiscence, although marginal cells do not appear modified as occurs in *Partitatheca*. These valves, if indeed present, would be of unequal size. However, the sizes and shapes of the predominantly elongate sporangial epidermal cells (Fig. 6n) are similar.

The monads are large (50-76μm) compared with hilate monads and have strongly folded walls covered in separated to closely-spaced coni, microconi and micrograna (Fig. 6o, p). An unusual feature noted in both light microscopy and TEM is the fusion between tips of the sculptural elements on adjacent spores (Fig. 6q) with, in places, a very thin layer connecting the junctions (Fig. 6r). Such spores have not been recorded in dispersed assemblages.

3. Discussion on relationships and affinities

Our use of groupings, based on sporangial and spore characters, indicates to some extent our broad conclusions on their relationships. In particular, a major perceived distinction between producers of permanent polyads and those with separated products is emphasized. The relationships among tetrad producers are less clear cut.

In the various species of *Partitatheca*, there is a distinct lineage of dyad and tetrad producers that combine characters of tracheophytes and bryophytes (Table 1; Fig. 1). Unique features are the presence of a layer that surrounds the entire polyad and complete fusion of the proximal walls of each polyad member, thus viable dispersed monads are never produced. The complex ultrastructure of the spore wall that is seen in the older dispersed spore examples implies links with some of the oldest embryophytes and possibly hepatics, although the limited sporophytic branching and the presence of stomata support a more derived affinity (Fig. 1). Indeed the combination of stomata and dispersed polyads supports the inference that basal stomatophytes possessed distal spore germination.

By contrast, in *Lenticulatheca* the dyads do not possess enclosing layers and separate within the discoidal sporangia before dispersal. The Lochkovian locality has also yielded similarly constructed sporangia which contain monads with similar sculpture but differ in the possession of trilete marks (Fig. 5p, q, r, s) (Morris *et al*., 2011). Such spores belong to the *Streelispora – Aneurospora* morphon in dispersed assemblages and are particularly significant because they are recorded in subspecies of *Cooksonia pertoni* (Fanning *et al*., 1988; Edwards *et al*., 1995a). A new genus, *Paracooksonia*, was erected to emphasize differences in sporangial characteristics (Morris *et al*., 2011). In the basal tracheophyte, *Cooksonia*, a discoidal spore mass is covered at maturity by a uniseriate wall comprising a single layer of cells distally while the multicellular subtending axis widens below the sporangium.

There are thus three groups of small plants with discoidal terminal sporangia united in their possession of monads with a bi-layered wall construction. In each group, distal spore walls range from laevigate to apiculate. It could be argued that differences in the tissues enveloping spore masses could be taphonomic, namely that decay of wall tissues could result in cuticle enveloped masses of spores. However, a prominent cuticle is not a characteristic of well preserved sporangial walls in *Cooksonia*, and a cellular construction has never been found in the hilate monad group. Nor is there a cuticular lining to the sporangium cavity in *Cooksonia pertoni*, although it has been recorded elsewhere (Morris *et al*., 2012b). We suspect that in *Paracooksonia* and *Lenticulatheca* the original sporangial walls were fleshy, i.e. composed of very thin-walled parenchymatous tissue with low fossilization potential, but surrounded by a thick cuticle. We discount the possibility that the wall was still developing, because the spores are mature. Regardless of these uncertainties, we are convinced that the plants in the *Lenticulatheca* complex are closely related to the basal tracheophytes (Fig. 1).

The discoidal sporangia containing permanent sculptured tetrads belonging to *Acontotetras* share some similarities to those in this lineage, including one with a cooksonioid-like sporangial wall (Fig. 6e). However, the tetrads to not possess a clear bi-layered wall construction (Fig. 6d) as observed in the monad equivalents described above. There is a suggestion of bi-layering in one specimen, but is based on a very thin outer layer that encompasses the entire tetrad (Fig. 6k, l), which was interpreted as an envelope. Without good TEM sections and more specimens we can only tentatively suggest that they were related to this lineage.

The relationships of the remaining sporangia, all represented by a single specimen, are also difficult to assess. Those with two valves (Fig. 4e-j) may well be close to the *Partitatheca* complex, the relationship finding support in the complex wall construction of NMW99.19G.2 and that the *in situ* spores are assigned to *Velatitetras* sp. (Fig. 4i). A second specimen (NMW99.11G.2) contains *Cheilotetras* sp., but the sporangial wall cells are smaller and far more numerous (Fig. 4e).

Even more difficult are specimens where we have no evidence of dehiscence. Particularly intriguing is *Grisellatheca salopensis* (Edwards *et al*., 1995b; Edwards *et al.*, 1999), the first mesofossil in which permanent laevigate tetrads, probably best assigned to *Cheilotetras* sp., were recorded (Fig. 7a, b, c), Certain anatomical features, including a single putative elater and the possibility that sporangial tissues were embedded in the tips of a bifurcating gametophyte, persuaded of affinities with the hepatics, but better preserved specimens are needed to substantiate this.

The three remaining illustrated specimens are united in the possession of tetrads with ‘ornamented’ envelopes assignable to three species of *Velatitetras*. However this does not indicate a close relationship even in the two examples where the outer layer is closely adherent or fused. The specimen shown in Figure 7g comprises the bases of two sporangia

with few spores (Fig. 7h), that show complexity in wall ultrastructure (Fig. 7i) that is comparable to those within the *Partitatheca* complex, leading to the possibility that the fertile regions of the specimen represent the bases of valvate sporangia. By contrast, the walls of the tetrads in specimen NMW96.11G.4 (Fig. 7j, k) are homogeneous (Fig. 7l). The sporangium itself, being discoidal and covered by cuticle, is reminiscent of the *Lenticulatheca* complex, but the nature of the spores precludes such a relationship. Thus *Velatitetras*, as defined by palynologists, was clearly produced by a number of plants of different affinities.

4. Dyads v. tetrads

These recent studies indicate that sporangia contain either monads, dyads or tetrads, and that fossils of similar architecture contained monads that were produced either from dyads or tetrads. There are never mixtures, inferring strict genetic control, with the possibility that the same species could produce polyads or monads at different times, be this on the same plant or in different populations. The latter has been attributed to environmental conditions by a number of workers, although there has been sometimes a certain lack of clarity resulting from the use of the terms taxa and 'plant' (? individual specimen v. clone v. species etc; e.g. Hemsley, 1994; Richardson, 1996a, 2007; Lavender & Wellman, 2002; Steemans *et al*., 2012). Lavender & Wellman (2002) had hypothesized that the great abundance of tetrads as compared with trilete spores at a number of Lochkovian localities indicated that the same 'taxa' produced different configurations at different times in response to ecological factors, rather than reflecting a different biological origin. This builds on Gray's contention of the importance of tetrads compared with the more easily dispersed triletes in founder populations under stressed environments (Gray, 1985). It is of some interest here that Visscher *et al.* (2004) reported a proliferation of lycophyte microspore tetrads in the dispersed spore record coincident with the end-Permian crisis, there associated with postulated increased UV

radiation. Steemans *et al*. (2012) extended such comparisons to include dyads and very strongly advocated that the type of spore produced by basal embryophytes depended on environmental factors and "probably do not reflect their biological affinities alone." Thus they noted clear morphological relationships between *Cymbohilates cymosus* Richardson, 1996a and *Chelinohilates erraticus* Richardson, 1996a (tetrads, dyads, alete monads) and *Cymbosporites stellospinosus* Steemans, 1989 and *Chelinospora cassicula* Richardson & Lister, 1969 (trilete monad), respectively, and between *Cymbohilates disponerus* Richardson, 1996a (alete monads, dyads), *Acontotetras inconspicuis* Richardson, 1996a (tetrad) and *Cymbosporites proteus* McGregor & Camfield, 1976 (trilete monad). Our own work broadly agrees with such pairings between dyads and monads (e.g. *Artemopyra brevicosta* Burgess & Richardson, 1991 and *Emphanisporites protophanus* Richardson & Ioannides, 1973; *Velatitetras reticulata* Burgess, 1991 and *Abditusdyadus histosus* Wellman & Richardson, 1996), although our ultrastructural evidence links somewhat different species and thus provides biological support for such groupings. In the dispersed spore record there is ultrastructural evidence for close relationships between Upper Ordovician dyad *Abditusdyadus histosus* (identified as *Segestrespora membranifera* in Taylor, 2001) and tetrad, *Velatitetras reticulata*, leading to Taylor (2000, 2001) to comment that the producers were the same plant or group of plants.

However, we are not so convinced of a developmental relationship between tetrads and dyads. Steemans *et al*. (2012) suggested such a relationship might exist between *Cymbohilates baqaensis* Breuer *et al*., 2007 and *Cymbosporites dammamensis* Steemans, 1995, because some of the former show a tear in the hilum that is roughly triangular and mimics a trilete mark, with inference that it too developed from a tetrad. We consider such a shape to be fortuitous and not uncommon in dispersed hilate monads.

Our results on the *Cooksonia – Paracooksonia - Lenticulatheca* complex are particularly relevant to the hypothesis that 'plants', presumably ecotypes, produced different spore configurations under different environmental conditions. That all these taxa grew at the same time is self evident, but the fossils are allochthonous and represent the remains of plants that grew in a range of habitats within the catchment area of the river systems. The small number of the cuticularised sporangia containing trilete spores of the *Streelispora - Aneurospora* complex (*Paracooksonia*) and hilate spores belonging to *Cymbohilates* (*Lenticulatheca*) compared with the sporangia of *Cooksonia pertoni*, perhaps indicate that *Lenticulatheca* and *Paracooksonia* colonized areas further from the depositional area, with *Cooksonia pertoni* in its vicinity. On the other hand it could be argued that the latter had more resilient sporangial walls. Consideration of relative numbers of their spores in the dispersed spore record is not helpful. Members of the *Streelispora - Aneurospora* complex dominate the record but the relative contributions of the two cooksonioid genera cannot be distinguished. However the numbers of ornamented hilate monads are higher than might be expected from the mesofossils, even allowing for the fact that the spore rain is derived from a wide geographical area. Indeed, Richardson (2007) in an attempt to use palynological and lithological data to gain a better understanding of the regional vegetational distribution in the Welsh Basin in Early Devonian times, had earlier commented on the relatively high percentages of ornamented monads (cryptospores and triletes) compared with laevigate hilate monads in sediments deposited in the flood plains of meandering rivers. This he attributed to the diverse vegetation growing in varied ephemerally wet habitats and contrasted it with the high percentage of laevigate hilate monads which were recovered from sediments deposited on alluvial plains subjected to occasional marine inundation and hence thought to derive from coastal vegetation. Studies on *in situ* spores as described here will allow further refinement of the data sets and hence deductions on the source plants.

IV. Evolutionary overview

Having identified the spores isolated from the majority of fertile specimens from the Lochkovian (see Table 2) and Silurian localities in the Anglo-Welsh Basin, comparisons with the same or closely related taxa in contemporary or earlier dispersed assemblages (Fig. 9) allow deliberations on the history of these early land plants, even in the absence of meso- and megafossils. However, before interpreting the miospore record in this way it should be recognised that, until relatively recently, few stratigraphical palynologists outside the oil industry have recognized reworking problems and hence the pitfalls of accepting ranges of species without question. An excellent example of such reworking occurs in the Emsian sequences of the Whitney Borehole (Richardson & Rasul, 1978, 1979) where species of the genus *Emphanisporites* occur in reverse order to the established occurrences. However, with care, reworked palynomorphs can be a useful source of dynamic data providing evidence for basin tectonics. Pulses of uplift in the Caledonian uplands to the north and west of the Anglo-Welsh Basin, a major source of Lower Old Red Sandstone sediments (Allen & Crowley, 1983; Allen, 1974, 1985), caused reworking from proximal landscapes into fluvial systems. Richardson has observed evidence for these pulses of uplift in the dispersed spore record, from influxes of reworked spores that are noted particularly at four stratigraphic levels. The first influx occurred in the lowermost Lochkovian, where species characteristic of the upper Ordovician and lowermost Silurian frequently show a spatially erratic and partly discontinuous distribution. After a period of quiescence, a second level is noted near the top of the Ditton Formation (late Lochkovian), where the palynological assemblages, which may consist entirely of marine acritarchs, occur within coarse fluvial sediments, thus inconsistent with their sedimentary environment. Slightly higher in the sequence these acritarch-rich

assemblages are associated with rocks containing pebble-sized clasts bearing marine macrofossils. By the late Lochkovian and into the Pragian these tectonic pulses occurred with increasing intensity as reflected in the abundance of reworked spores. In the Senni Formation of the Brecon Beacons (Pragian) (Hassan, 1982) they are derived mainly from Lower Palaeozoic strata and occur commonly in most sediments. Finally, in Emsian sediments of the Witney Borehole, Lower Palaeozoic marine microfossils are so abundant (Richardson & Rasul, 1978, 1979) that they are often the most frequent fossils present.

Issues with reworking aside, the new information on *in situ* spores is of value not only in reconstructing disparity in Lochkovian vegetation on regional to global scales, where mega- and mesofossil evidence is lacking, but also in tracing the history of its various components. Here we must emphasise that we are concerned only with spores. We cannot infer, because of the possibility of sequential acquisition of other characters, such as stomata and branching sporophytes, that earlier plants were identical to Upper Silurian and Lochkovian representatives. However the approach has been adopted for the tracheophytes, in that the presence of trilete spores in the Middle Ordovician (Steemans *et al*., 2009) is the bench mark for the appearance of the tracheophytes and, as it includes laevigate forms attributed to *Ambitisporites* Hoffmeister, 1959, for the origin of the *Cooksonia* complex, because *Ambitisporites* was recorded in *Cooksonia pertoni* of Přídolí age (Fanning *et al*., 1988). Their ancestors might be sought in the Ordovician producers of laevigate, non-enveloped tetrads (e.g. *Tetrahedraletes* complex) but these were probably derived from a number of taxa as indeed were species of *Ambitisporites*. Specimens assigned to *Tetrahedraletes* differ in the relative dimensions of distal and proximal walls, degree of fusion of the latter, extent of indentation at the margins of contact faces, convexity vs. concavity of the distal surface (Strother *et al*., 1996) and the nature of the shape of the equatorial thickening in section. However, ultrastructural studies have been disappointing (Taylor, 1995b, 2002). Most

Ordovician to Silurian specimens examined usually showed homogeneous walls, but sometimes occasionally spongy, apart from one with occasional sporadic linear structures parallel to the surface and another where a thick homogeneous wall is external to a highly convoluted single lamina (23-70 nm thick) that surrounds the lumen (Taylor, 2009). Thus the bi-layered wall that characterises spores in the *Cooksonia pertoni* complex is first seen in *in situ* triletes (*Ambitisporites*, Rogerson *et al*., 1993) and dyads (*Laevolancis divellomedia* type A, Wellman *et al.*, 1998b). Steemans *et al*. (2012), in attempting to trace such lineages, mentioned that some *Tetrahedraletes* spores showed a tendency to become detached and *Rimosotetras problematica* Burgess, 1991 is characterised by loosely attached spores. In fact Gray (1991) suggested that permanent tetrads tend to break apart revealing proximal triradiate mark. Evidence for probable physical tearing apart of a tetrad comes from Late Ordovician monads where a tear on the proximal face mimics a trilete mark (*Imperfectotriletes* (?*Ambitisporites* Richardson, 1988) Steemans *et al*., 2000). *Imperfectotriletes varvdovae* being crassitate (equatorially thickened) is closest to *Ambitisporites* sp. in *Cooksonia pertoni*. However there is no supporting ultrastructural evidence.

The earliest records of sculptured trilete spores in the Mid - Late Ordovician comprise *Synorisporites*, either with low verrucae or convolute muri, a ?*Synorisporites* and *Aneurospora* with grana or small verrucae (Steemans *et al*., 2009). This suggests the presence of further members of the *Cooksonia* complex much earlier than previously known (Homerian; Richardson, 1988; Burgess and Richardson, 1991) and, more importantly, the earlier diversification of the presumably vascularised embryophytes (Steemans *et al.*, 2009). Returning to our hypothesis that the cooksonioid complex contained plants with either separating dyads or trilete spores, the records of hilate monads with a bi-layered wall construction can be traced back only to the Přídolí (Fig. 5a-c; Wellman *et al*., 1998b), despite

the fact that laevigate forms, represented by *Laevolancis divellomedia*, appeared in the dispersed record in the Early Silurian (Rhuddanian) (e.g. Steemans *et al*., 2000). This is partly due to the lack of sectioning studies on older examples, but also because the range of ultrastructure noted in spore masses and sporangia of *L. divellomedia* from the Přídolí (Wellman *et al*., 1998b) indicates diverse affinities of the producers, making it impossible to identify more precisely the older dispersed examples on morphology alone. However, Wellman et al suggested that the monads, *L. divellomedia* were 'derivatives' of certain *Dyadospora* (obligate dyads) and we would postulate that based on the bilayered nature of its relatively simple ultrastructure and the absence of the outer wall that completely surrounds the dyad, of *D. murusattenuata.* type II (Taylor 1997). On such tentative evidence stem group tracheophytes might be represented in the earliest spore assemblages although we should emphasise that the earliest examples of *D. murusattenuata* with type II anatomy are found in the Lower Silurian. Similar reasoning might be employed to link *Dyadospora murusattenuata* type I, with the *Cymbohilates horridus* complex (Fig. 2a, d) extending this lineage in which the spores never separated into the upper Ordovician. However, as with *Laevolancis*, the types cannot be determined from one another by external morphology alone and more sectioning studies of older examples are required.

Considering further this second lineage of plants possessing permanent tetrads and dyads, sculptured forms of the latter, belonging to the *Cymbohilates horridus* complex or *Cymbohilates cymosus*, are only recorded in the Lochkovian, while Silurian valvate sporangia contain permanent laevigate dyads assigned to *Dyadospora murusdensa*, some with, but incompletely elucidated, wall ultrastructure (Fig. 3r; Wellman *et al*., 1998a) of complexity broadly similar to that observed in dispersed specimens of *Dyadospora murusattenuata* type I from the Upper Ordovician sectioned by Taylor, 1997, as discussed above.

Of the permanent tetrads, the laevigate *Cheilotetras* sp. occurs in two, albeit Lower Devonian, valvate sporangia (Fig. 4a-d, e-g; Edwards *et al*., 2012b). The genus *Cheilotetras* is recorded as far back as the early Wenlock (e.g. Wellman & Richardson, 1993), but so far have produced disappointing sections, although some with gross layering (Fig. 4g). However, Přídolí trilete monads and tetrads of *Cymbosporites echinatus* (Richardson & Lister, 1969) were thought close to the *Cymbohilates horridus* complex because of similarities in the ornament on distal surfaces. Johnson & Taylor (2005) demonstrated a bi-layered wall construction in which an electron-dense layer extends around the whole spore and a complex outer wall is confined to the equator and distal wall (Fig. 2j). The latter corresponds to the surface which would be exposed in the tetrad. This layer is tripartite, the outer homogeneous and extending into the sculpture, the middle with a spongy texture and the inner with lamellate construction. It thus broadly corresponds to the layer that extends around both units of the permanent dyad in *Cymbohilates horridus*. Isolated monads almost invariably show collapsed poorly preserved proximal faces, the trilete mark either absent or comprising very narrow laesurae, often confined to the equatorial regions, or represented only by a tear that mimics its shape, all features suggestive of poorly controlled separation. It is tempting to compare this with remnants of the fused proximal walls noted in torn apart dyads in *Cymbohilates horridus* (Richardson, 1996a, Pl. 6, fig. 1), although impossible to pontificate on the viability of the spores in this developmental scenario.

Regarding the enveloped tetrads and dyads, spores belonging to Lochkovian *Velatitetras* sp. (Fig. 2, g ii, iii) within an elongate valved sporangium and dispersed Upper Ordovician forms of *Abditusdyadus* (*Segestrespora*) (Fig. 2e) possess thick envelopes, some with internal structure (Fig. 2g ii). If these envelopes are considered homologous to the outer enveloping wall, they show similarities in ultrastructure with the *Cymbohilates horridus* complex and *Dyadospora murusattenuata* type I. Therefore, we tentatively hypothesise the homology

between the thick envelope in these examples and the outer enveloping wall in the *Cymbohilates horridus* complex.

Dispersed records show a global decrease in numbers of permanent dyads and tetrads throughout the Silurian leading to almost complete disappearance in the Lower Devonian (Fig. 9). Anomalous records of permanent tetrads (Filipiak, 2011) and dyads (Breuer *et al*., 2007) in the Emsian may be due to reworking. As indicated below and based on the assumption of possession of sex chromosomes, there were advantages in terms of reproductive biology for fertilization in gametophytes developed from tetrads. Negative aspects include increased homozygosity and limitations on dispersal. The latter is improved in dyads, but the chances of fertilization are reduced. In both groups their permanent nature would be barriers to germination, especially if an envelope is present. Indeed Steemans *et al*., (2012) postulated that changes in thickness frequency of envelopes declined to facilitate germination. Exit of the germination tube would presumably have been via distal surfaces, where there are no specially modified sites. However, our sections through a spore mass (Fig. 8a) of loosely adhering tetrads (Fig. 8b) show adherence to separation of the thin proximal walls (Fig. 8c, d) and it is possible that even in the absence of a well defined trilete mark, the latter sometimes represented by a weakly developed ridge (Fig. 8e, f), the germination tube could have exited here and grown between individual spores to the exterior. Taylor (2002, p.334) had earlier speculated that such a protected proximal surface 'might have been "preadapted" to accommodate a specialized zone of weakness', although he concluded that in trilete spores, germination via a 'proximal suture' must have occurred when that surface became exposed. We therefore conclude that the torn apart monads noted in dispersed assemblages, with incomplete proximal surfaces, were not viable.

As for the smooth and ornamented hilate monads, recent studies have shown that they are linked to trilete spores, with similar ultrastructure, hence to the parent plants in the *Cooksonia*

complex. The spores and megafossils share a similar stratigraphic distribution across the Welsh Basin, disappearing in the mid to late Lochkovian, which suggests that differences in meiosis and inferred reproductive biology were not responsible for their demise. Instead, it has been noted that there was an increase in numbers of retusoid spores in the dispersed records across the basin at this time, some known to be derived from zosterophylls (Edwards & Richardson, 1996), plus the appearance of megafossils of *Zosterophyllum* (summary in Edwards & Richardson, 2004), which show a departure from a strictly determinate growth form. This led to the suggestion of competitive displacement (Edwards & Davies, 1990), with the progressive invasion of the plant habitats of the cryptospore-producers and rhyniophytes. This radiation of the zosterophylls and higher plant taxa into the Anglo-Welsh Basin during the late Lochkovian may have been related to a shift towards increased rainfall and a wetter climate in the Lower Devonian (Thomas *et al*., 2006; Hillier *et al*., 2007; Morris *et al*., 2012c).

V. Variation in the meiotic process

In modern land plants the spores are dispersed as single units (monads) whereas the cryptophytes show much greater diversity, including cryptospores dispersed as dyads and tetrads with or without a second enveloping membrane. Hemsley (1994) pointed out that the origin of this diversity could be explained by the nature of the process of meiotic cell division, which when coupled with changes in the timing of the synthesis and deposition of sporopollenin (Blackmore and Barnes 1987) could give rise to all of the morphologies observed among the cryptospores. Dyads might arise if during Meiosis I cytokinesis were followed by separation of the products to form monads, then depending on the timing of sporopollenin synthesis and deposition during Meiosis II either permanent dyads with an outer enveloping membrane or hilate monads would result (Fig. 10). Tetrads would form if

the products of Meiosis I did not separate and were followed immediately by Meiosis II. Again, the timing of sporopollenin synthesis and deposition during Meiosis II would determine whether monads or permanent tetrads were the end products (Fig. 10). Two lines of evidence strongly imply that these cryptospore types were a normal part of the developmental repertoire of early land plants. First, with few exceptions (e.g., Richardson 1996b), cryptophyte sporangia never contain mixtures of dyad types or dyads and tetrads, indicating that there was strict genetic control over their development. Second, cryptospores were a prominent element of early palynomorph assemblages, persisting for over 60 million years. Today, normal meiosis in basal land plants follows the tetrad path resulting in sporopollenin coated monads, which has led to the unchallenged contention that the obligate tertrahedral tetrad is the plesiomorphic state in land plants (e.g., Gray 1991, 1993). This hypothesis was proposed when the nature of the dyad-producing plants was unknown. Now that they have been documented in cryptophyte sporangia, the possibility that dyads are plesiomorphic in land plants must be given serious consideration. Neither phylogeny nor stratigraphy provide a clear answer. Dyads are almost as abundant as tetrads in early palynomorph assemblages, and like tetrads they have been documented *in situ* in cryptophyte sporangia, however the precise phylogenetic relationships of most early cryptospores to major embryophyte clades remain unclear. Stratigraphically, the earliest palynomorph assemblages comprise monads, dyads, and tetrads, with and without enveloping membrane (Steemans *et al*., 2010; Rubinstein *et al*., 2010). So, we cannot say whether the dyad or the tetrad came first. From the perspective of developmental biology, meiosis in modern bryophytes is seemingly a better fit to the tetrad hypothesis. During sporocyte development the tetrahedral form marking future spore domains begins to develop precociously, with the process of cytokinesis commencing prior to meiosis (Brown & Lemmon 2011). There is no indication of separation of cell products during Meiosis I as would be required for dyad

formation (Fig. 10). Although informative, these observations tell us only about the plesiomorphic state for crown group embryophytes, whereas the cryptophytes hint at greater diversity in the bryophyte, vascular plant and embryophyte stem groups (Fig. 1). The diversity of cryptospores in the early fossil record testifies to a far greater versatility in meiosis among the basal embryophytes than is evident in living plants.

The particular geometry of cryptospores, including their size, the number of units they contain, and the presence or absence of an enveloping membrane, have potential consequences for cryptophyte biology. Many authors have commented that some characteristics of tetrahedral tetrads are typical of founder populations. These include small size and production in large numbers. Tetrad size averaged less than 27µm during the Ordovician increasing to 40-50µm and greater during the Llandovery (Gray 1991), and Wellman *et al*., (2003) estimated that a small (0.3 x 0.23mm) sporangial fragment from the Ordovician contained over 2,500 tetrads.

Cryptospore geometry is also potentially significant in sexual reproduction, but only for species with gametophyte dioecy. We do not know how gender was expressed in the cryptophytes, but it is estimated that about 50% of living bryophytes exhibit gametophyte dioecy (Jesson & Garnock-Jones, 2012), in which the male and female sex organs form on different individuals, and gender is established by sex chromosomes that are segregated during meiosis. The obligate tetrad-producing living hepatics such as *Riccia*, *Sphaerocarpos* and *Cryptothallus* are dioecious. Dispersed tetrads therefore contain two male and two female spores, facilitating sexual reproduction through selfing. In dyad producing cryptophytes, segregation of sex chromosomes during Meiosis I would result in dispersal units of the same sex. Therefore, from the perspective of sexual reproduction, dyads and monads are functionally equivalent, whereas tetrads have the advantage of transporting both sexes to the same place. On the other hand, if the cryptophytes were gametophyte co-sexual, they would

have been hermaphroditic, and therefore all cryptospore forms were functionally equivalent in terms of sexual reproduction. So, different combinations of spore type and gender expression may have been advantageous to founder populations. For plants with gametophyte dioecy, the obligate tetrad would have enabled intergametophytic selfing (autogamy). For plants that were gametophyte co-sexual cryptospore geometry is irrelevant because all spores produce hermaphrodites leading to intragametophytic selfing (automixis). It has been argued that selfing in founder populations might explain the evolutionary stasis of the cryptospores themselves (i.e., their conservative form) throughout the Ordovician (Wellman & Gray, 2000; Steemans et al., 2012), because autogamy and automixis lead to increasingly homozygous individuals and inbreeding depression. A further consequence of cryptospore geometry relates to germination. In trilete monads, the trilete feature is a weakness in the proximal face of the cell wall that facilitates spore germination. No such equivalent feature exists in obligate dyads and tetrads. The proximal faces are fused, so germination can only occur through the distal faces. Emergence of a germination tube would have been further hampered by the presence of the outer envelope. Indeed Steemans *et al*., (2012) considered that this double hurdle in germination was responsible for near disappearance of dyads and tetrads during the early Silurian, whereas this period was characterised by the proliferation of trilete monads.

The demise of the cryptophytes is still poorly understood in causal terms. Cryptospores were produced well into Devonian times, and occasionally palynomorph assemblages document the proliferation of tetrads (although the majority of these probably derived from tracheophytes), a phenomenon that has been linked to times of environmental stress (e.g. Lochkovian, Lavender & Wellman, 2002). Whereas the number of permanent dyads declined, the diversity of hilate monads, particularly smooth forms, was sometimes almost comparable to the diversity of trilete spores. This persistence of cryptospores for over 60

million years and their co-occurrence with trilete monads for at least half of this period indicates that the causes of their decline had little to do with their reproductive biology. Ecological changes during the Early Devonian may provide a more fruitful line of investigation (Edwards & Davies, 1990). During this period vascular plants were diversifying on land, initiating a rapid increase in plant size that led to the development of the first forest ecosystems by the Middle Devonian (Meyer-Berthaud *et al.*, 2010; Stein *et al.*, 2012). The cryptophytes were very small organisms, and they would have fared poorly in competition with much larger vascular plants for light and other resources. The development of a land flora dominated by vascular plants represents a major environmental change with significant consequences for life on land and for key Earth Systems (Kenrick et al., 2012). The demise of the cryptophytes may have been just one of several tangible consequences of the rise of the vascular plants.

VI. Spore wall formation and the nature of the envelope

Figure 2 summarises the variation in the complexity of ultrastructure in Ordovician to Lochkovian cryptospores. Regardless of this disparity, which we must emphasise is based on mature dispersed and *in situ* spores, of the four types of wall development summarised by Blackmore & Barnes (1987), we favour sporopollenin deposition on white line centred lamellae, as seen in almost all investigated bryophytes (Brown & Lemmon, 1990; but see Brown & Lemmon, 1984 for *Andreaea*) and basal tracheophytes (Tryon & Lugardon, 1991) as the pleisomorphic condition, but evidence of such organisation can be obliterated by further sporopollenin deposition. However the homology of the various layers, including the envelope (sometimes called a membrane), merits further discussion. In some spores, the latter is a discrete layer, which may surround tetrads, dyads or monads, is adherent to or separate to varying extents from the exospore and, apart from folds, lacks ornament. Its inner surface is

usually smooth. Although its resilience to decay suggests a similar composition to sporopollenin, its chemistry is unknown and in some specimens (e.g. *Acontotetras* within a fragmentary discoidal sporangium NMW2012.17G.1, Fig. 6l), there is a differential response to staining from the spore wall. It usually has a homogeneous ultrastructure. Exceptions include the envelopes of *Velatitetras* and *Abditusdyadus / Segestrespora*, which are significantly thicker and may not be homogeneous, for example in specimen V.68196(2) (Fig. 7p). The outer surfaces may show folding, often interpreted as an ornament comprising regular to irregular reticulate muri (e.g. *Velatitetras cristata*, *V. retimembrana*, *Abditusdyadus histosus*). They also show significant separation from the exospore and internal structures such as voids (Fig. 2g ii), or inward projections (Fig. 2g iii). Edwards et al., 2012a illustrate sections through the *Cymbohilates horridus* complex that suggest the outer sculptured layer with complex ultrastructure, which is usually very closely adherent to the exospore, shows signs of separation and hence is possibly homologous to the thick envelopes of *Segestrespora* and *Velatitetras*, possibly with a similar developmental pathway. This would account for the vacuolated layer and inwardly directed projections within certain specimens of *Velatitetras* sp. (Edwards et al., 2012b).

Although common in early assemblages, enveloped spores decrease in number abruptly near the Aeronian/Telychian boundary, around the time when trilete spores were increasing in numbers (Steemans *et al*., 2012). Nevertheless they persist into the Lochkovian, including our own discoveries in the mid MN bio-zone, as well as new species of *Abditusdyadus* and *Velatitetras* (*Nodospora*) *retimembrana* Wellman & Richardson, 1996, lower MN zone. For the envelope, a number of authors have postulated its origin via a secretory tapetum to form a kind of perispore, although this layer surrounds individual monads in extant mosses and ferns, and a tapetum is not found in liverworts (Gray, 1985; Johnson, 1985), or the remains of the spore mother cell wall (synoecosporal wall; Taylor & Strother, 2008). Here we

adopt a more parsimonious approach and suggest that it was produced, as was the exospore wall, immediately outside the plasmalemma, in the case of the tetrad possibly before any cytokinesis, and in that of the permanent dyads, following the separation of the two cells resulting from cytokinesis after the first reduction division (Meiosis 1). This would be followed by further plasmalemma secretions resulting in a usually layered exospore with variation in appearance at maturity depending on degree of obliteration of original ultrastructure by sporopollenin. This wall would have completely enclosed the developing tetrad or dyad, but following cytokinesis that produced four or two sets of two cells, further plasmalemma activity would have produced a wall around each spore. The trilete and hilate monads with a bi-layered exospore lack both envelope and an enclosing common outer exospore, but would via plasmalemma activity produce first an outer, and then an inner layer around both distal and proximal surfaces after the separation into monads.

These postulated developmental pathways will be discussed in light of the hypotheses of previous workers who suggested *inter alia* that the envelope is equivalent of the spore mother cell wall or synoecosporal wall (Taylor & Strother, 2008), that a polysaccharide special cell wall was secreted by the plasmalemma after the products of the first meiotic division in *Dyadospora murusdensa* (Taylor, 1996), detailed comparisons with processes described in a relatively small number of extant basal embryophytes (Blackmore & Crane, 1988; Villarreal & Renzaglia, 2006; Brown & Lemmon, 2011; Wallace *et al*., 2011). The traces of an amorphous outer layer in *Cymbohilates horridus* (Fig. 3e) (Edwards *et al*., 2012a) and *Dyadospora murusattenuata* type I (Taylor, 1997) might represent the remnants of the special cell wall.

Returning to the possibility of tapetal activity, although here we discount the possibility that it was responsible for an envelope, our earlier studies on retusoid spores (*Retusotriletes*) associated with the basal lycophytes (*Resilitheca salopensis* Edwards *et al*., 1995c;

Sporathylacium salopense Edwards *et al*., 2001) demonstrated granular material adhering to the spore surfaces and the innermost surface of the sporangium wall. We interpreted these structures as tapetal residues with possible homologies to the Ubisch bodies in pollen grains (Pacini, 1990) and globules and spherules in extant homosporous lycophytes (Tryon & Lugardon, 1991). In our studies on cryptospores we have found similar structures on both sites in *Ficoiditheca aenigma* (Fig. 8g, i, j, k), a permanent dyad-producing plant (Fig. 8l) from the Lower Devonian locality, with stomatiferous bifurcating axes terminating in sporangia, which unlike the valvate forms, dehisced distally into a number of small valves (Fig. 8h) (Morris *et al*. 2012a). The dyad exospore comprised three homogeneous layers with irregular clusters of granules incorporated in the outer (Fig. 8m, n). This combination of characters is unique and probably representative of a further distinct clade with grades of organisation similar to those in *Partitatheca*, except for the spore ultrastructure and the putative tapetal activity. Similar structures have also been noted on the surfaces of enveloped tetrads in a Lower Devonian specimen, NMW96.11G.3 (Fig. 7g, h; Edwards *et al*., 1999) and, although initially interpreted as an irregular microgranulate sculpture, similar structures were also observed over the inner surfaces of the sporangium wall in association with the large extra-exosporal fragments, thus suggestive of tapetal residues. An earlier, less convincing example is from the Přídolí at Ludford Lane, where spores with adhering clusters of granules (Fig. 8p) occur in an extensively elongate, sporangial fragment that is incomplete at both ends and partially surrounded by a smooth acellular cuticular layer (Fig. 8o). The hilate monads assigned to *Laevolancis divellomedia* possessed a layered wall, the inner lamellate surrounded by a thicker homogeneous layer with a further very thin layer present over the distal and equatorial region and bearing the granules (Fig. 8q, r). The latter are not present on the proximal faces as seen in *Retusotriletes*, thus deposition in this case must have preceded separation of the dyad and thus less likely to represent tapetal material in the

conventional sense. Nevertheless, this again is a new combination of characters in cryptospore-bearing plants.

VII. Conclusions

1. Our recent studies of exceptionally well-preserved mesofossils from the Silurian-Devonian (Přídolí –Lochkovian) of the Welsh Borderland are beginning to reveal the source plants of many of the spores found dispersed in sediments of that age. We show that the enigmatic cryptospores were produced by minute plants that possessed a combination of features not found together in living species. The fossils are highly fragmentary, so many aspects of their overall morphology, biology and affinity still remain unclear. We propose to term these plants cryptophytes in order to recognize a level of organisation of basal embryophytes that does not fit within crown group liverworts, hornworts, mosses and vascular plants, and to provide a focus for further research and discussion. Cryptophytes comprises a grade of organization of plants producing cryptospores in sporangia, some of which might belong to the embryophyte stem group (Steemans *et al*., 2009) whereas others are more closely related to one or more embryophyte crown groups (Fig. 1). It is important to emphasize that cryptophytes are not bryophytes as is frequently implied in the literature (e.g., Wellman *et al*., 2003; Duckett *et al*., 2006). Such generalisations tend to be taken up unreservedly by the wider botanical community and are highly misleading. For example, Budke *et al*., (2012), in studying the cuticularised calyptra of *Funaria hygrometrica*, concluded that the 'role of the calyptra in desiccation prevention offers a functional explanation for calyptra retention during the 450 Myr of moss evolution…'. There is no evidence of calyptra in the cryptophytes or in any known fossil of the Palaeozoic Era. The newly emerging fossil evidence is more in line with the original interpretation envisaged in the pioneering work of Gray and Boucot (1977) who

considered cryptospores to have been the products of plants that were proto-hepatics or proto-bryophytes. The cryptospore-producing plants may be bryophyte-like in their size and in some aspects of their morphology (Richardson, 1992; Tomescu & Rothwell, 2006; Steemans et al., 2009; Kenrick *et al*., 2012), but much still remains to be learned about these as whole organisms, and little is yet known of their biology. Despite the fragmentary nature of the cryptophyte fossils, some distinctive groupings are beginning to emerge (Fig. 1). *Partitatheca* includes plants with bifurcating axes terminating in valvate sporangia bearing stomata. Spores are dyads with a laminated wall structure belonging to the dispersed cryptospore genus *Cymbohilates*. *Lenticulatheca* encompasses discoidal sporangia containing monads that are clearly derived from dyads that are also assignable to *Cymbohilates*. In addition, detailed comparative studies of cryptospores indicate that several features of the *Dyadospora murusattennuata* complex (i.e., absence of outer dyad envelope; bilayered wall) might link this group to the vascular plants. Further descriptive work on these mesofossil assemblages, and in particular the application of new, non-invasive imaging methods (i.e., synchrotron microtomography) (Friis *et al.*, 2007), is essential to developing our understanding of the cryptophytes and their relationships.

2. Research on the Anglo-Welsh Basin provides a detailed regional picture of the evolution of plant life on land. These sediments are the best in the world for a more or less uninterrupted sequence through the Upper Silurian (Přídolí) to Lower Devonian (Pragian), with an excellent biostratigraphic framework. Although direct fossil evidence of the cryptophytes comes from only two sites, there is an extensive and well-documented record of dispersed spores for the region. Major differences have been noted in the palynological assemblages between the Raglan Marl Formation (Přídolí to lowermost Lochkovian) and the Senni Formations (upper Lochkovian to Pragian) (Richardson & Lister, 1969;

Richardson *et al*., 1982; Hassan, 1982). Spores derived from larger vascular plants, mostly zosterophylls (i.e., basal lycophytes) diversified, and this was accompanied by a major decline of the cryptospores (Edwards & Richardson, 2004). This pattern was interpreted in ecological terms as one of local competitive displacement of cryptophytes and rhyniophytes by the larger zosterophylls (Edwards & Davies, 1990).

3. The patterns emerging from the Anglo-Welsh Basin provide insights into events on a regional scale towards the end of cryptospore evolution. A global perspective over the same and a more extended time interval is reliant solely on the record of dispersed palynomorphs. Since there is no corroborating evidence of *in situ* cryptospores elsewhere, this evidence should be interpreted cautiously. First, sampling of the dispersed palynomorph assemblages is biased towards sites in Laurussia, whereas sampling from Gondwana is particularly sparse (Steemans *et al*., 2010). Second, records of cryptospores pre-dating the mid Ordovician are controversial (e.g., Strother *et al*., 2004) because, although generally similar in form and with resistant walls, they lack the regular, well-defined arrangements of later tetrads and dyads. Third, although some early dispersed spore types have been identified *in situ* in cryptophytes and vascular plants (e.g., *Cymbohilates*, *Streelispora*, *Aneurospora*, *Velatitetras*, *Cheilotetras*) many have not. Fourth, the newly emerging fossil evidence on the morphology of the cryptophytes documented here comes from latest Silurian to earliest Devonian rocks. The key morphological features exhibited by these fossils (e.g., sporangia; and in some sporangial dehiscence, branched sporophytes, stomata), would have probably evolved sequentially on land and may not all therefore have been present in the cryptophytes of the Ordovician Period. Bearing these caveats in mind, spores attributable unequivocally to cryptophytes first appeared in the Middle Ordovician (Dapingian Stage; ca 470Myr) on the Gondwana

Plate, and subsequently in Avalonia, Laurentia, Baltica and finally South America through the Late Ordovician to Early Silurian (Steemans et al 2010). Diversity was greatest in the Late Ordovician and the earliest part of the Silurian (basal Llandovery), and it decreased through the Silurian. The cryptospores almost disappeared during the Lower Devonian, but plants from within the cryptophyte grade gave rise to the modern lineages of land plants. The demise of the cryptophytes is poorly understood in causal terms, but we suggest that this was related to major ecological changes brought about by the diversification and rapid increase in size of the vascular plants during the Early Devonian leading eventually to the evolution of the first forest ecosystems.

4. The fossil record of cryptospores testifies to a far greater versatility in meiosis among basal embryophytes than is evident in living plants. This diversity can be explained by the developmental process of meiotic cell division coupled with changes in the synthesis of sporopollenin and the timing of its deposition. Cryptospore geometry exhibits some traits that are characteristic of founder populations, including small size in early forms. Although gametophyte gender expression in cryptophytes is unknown, the dispersal unit of the permanent tetrad always ensures the possibility of sexual reproduction through either autogamy (gametophyte dioecious: intergametophytic selfing) or automixis (gametophyte co-sexual: intragametophytic selfing), whereas this is possible in dyads and monads only when gametophytes are co-sexual. Where gametophytes are dioecious, dyads and monads are functionally equivalent dispersal units, and this combination of gender expression and cryptospore form would not favour population establishment over long-distances. Dyads are almost as abundant as tetrads in early palynomorph assemblages, and our finding of dyads *in situ* in cryptophyte sporangia proves that this cryptospore type derives from land plants and that it was part of their normal meiotic repertoire. This finding challenges the long held consensus that the tetrad configuration, plus the

production of four haploid spores, was the archetypical condition in the pioneering land plants. The possibility that dyads are the plesiomorphic state in land plants should be given serious consideration.

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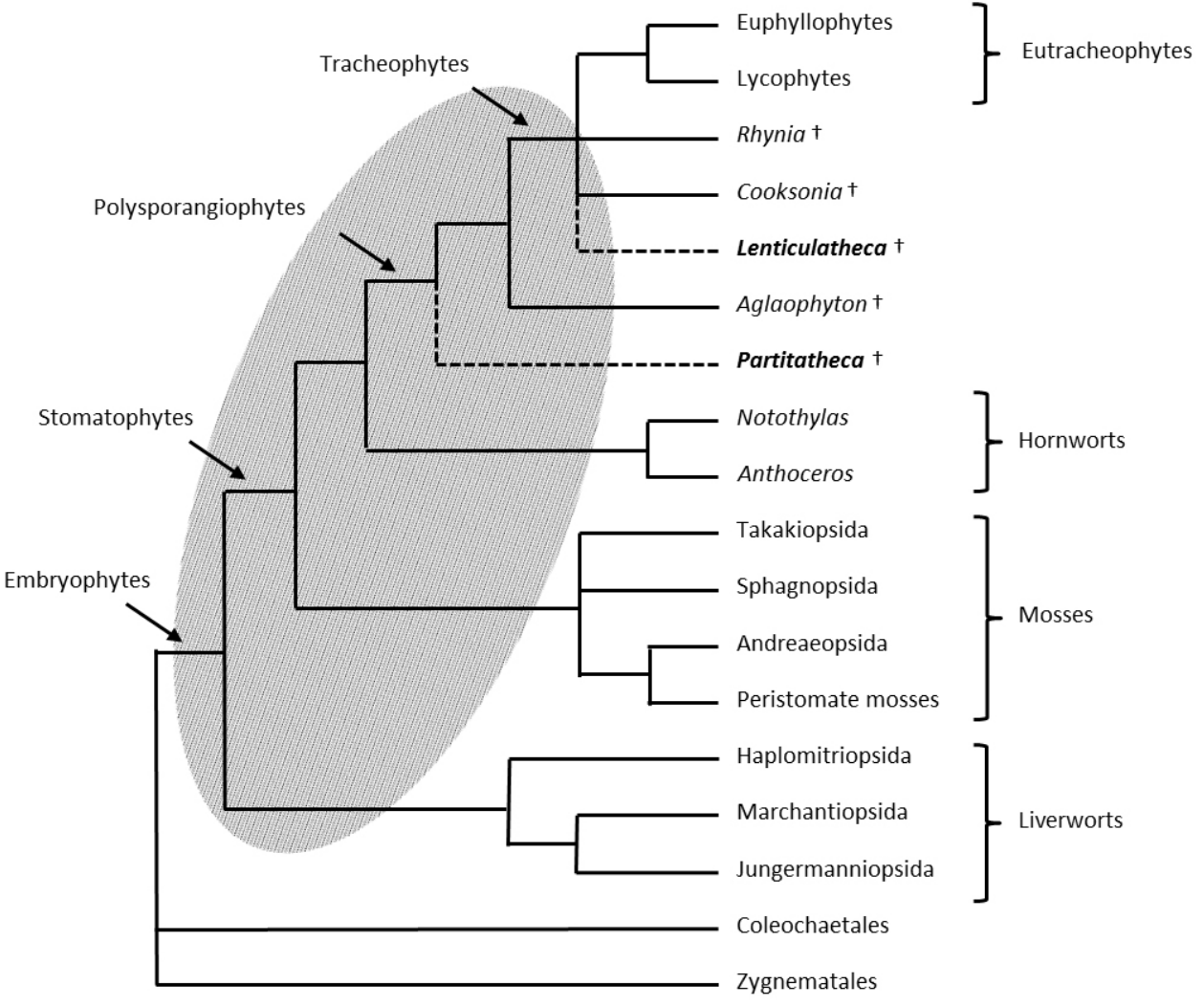
Table 1: Distribution of selected sporophyte and spore features in major basal land plant clades compared to the early cryptophyte fossil *Partitatheca*. X absent; ✓present; (✓) present in some; ✓ (few) rarely present.

	Liverwort	Hornwort	Moss	Tracheophyte	*Partitatheca*
Branching sporophyte	x	x	x	✓	✓
Valvate sporangia	✓ (few)	✓	(✓)	(✓)	✓
Stomata	x	✓	✓	✓	✓
Lamellae in spore wall	✓	✓	✓	✓	✓
Permanent tetrads	✓	x	✓	x	(✓)
Permanent dyads	x	x	x	x	✓
Trilete spores	(✓)	(✓)	✓ (few)	✓	x

Table 2: Review of *in situ* spores found in sporangia from Brown Clee Hill Lochkovian locality.

Genus / Type	**Species**	***In situ* spores**	**References**
Trilete producers			
Cooksonia	*pertoni* subsp. *pertoni*	*Ambitisporites* sp.	Fanning *et al*., 1988
	pertoni subsp. *apiculispora*	*Streelispora newportensis*	Morris *et al*., 2012b
		Aneurospora spp.	
	pertoni subsp. *reticulispora*	? *Synorisporites* sp.	Habgood *et al*., 2002
	banksii	cf. *Ambitisporites* sp.	Morris *et al*., 2012b
	hemisphaerica	*Ambitisporites* sp.	Edwards, 1996
Paracooksonia	*apiculispora*	*Streelispora newportensis*	Morris *et al*., 2011
		Aneurospora cf. *trilabiata*	
		Aneurospora sp.	
Tortilicaulis	*offaeus*	*Apiculiretusispora* sp.	Edwards *et al*., 1994; Morris *et al*., 2012b
Pertonella	sp.	*Retusotriletes coronadus*	Edwards, 1996
Tarrantia	*salopensis*	? *Retusotriletes*	Edwards, 1996
Resilitheca	*salopensis*	*Retusotriletes* sp.	Edwards *et al*., 1995c
Sporathylacium	*salopense*	? *Apiculiretusispora*	Edwards *et al*., 2001
Salopella	cf. *marcensis*	*Aneurospora* sp.	Edwards *et al*., 1994
cf. *Horneophyton*	sp.	*Emphanisporites* cf. *micrornatus*	Edwards & Richardson, 2000
Spheroidal sporangium		? *Iberoespora* sp.	Morris *et al*., 2012b
Circular spore mass		*Emphanisporites* sp.	Morris *et al*., 2012b
Cryptospore producers			
Permanent dyads			
Culullitheca	*richardsonii*	*Dyadospora murusdensa*	Wellman *et al*., 1998a
Fusiformitheca	*fanningiae*	Laevigate enveloped dyads	Wellman *et al*., 1998a
Partitatheca	*splendida*	*Cymbohilates horridus* var. *splendidus*	Edwards *et al*., 2012a
	horrida	*Cymbohilates horridus* var. *horridus*	Edwards *et al*., 2012a
	densa	*Cymbohilates horridus* complex	Edwards *et al*., 2012a
	cymosa	*Cymbohilates cymosus*	Edwards *et al*., 2012a
	sp.	*Chelinohilates erraticus*	Morris *et al*., 2012a
Ficoiditheca	*aenigma*	?	Morris *et al*., 2012a
Separating dyads			
Lenticulatheca	*magna*	*Cymbohilates allenii* var. *magnus*	Morris *et al*., 2011
	allenii	*Cymbohilates allenii* var. *allenii*	Morris *et al*., 2011
	variabilis	*Cymbohilates variabilis* complex	Morris *et al*., 2011
	mesodeca	*Cymbohilates mesodecus*	Morris *et al*., 2011
	? sp.	*Cymbohilates rhabdionus*	Morris *et al*., 2011
Permanent tetrads			
Grisellatheca	*salopensis*	*Velatitetras* sp.	Edwards *et al*., 1999
Discoidal		*Velatitetras* sp.	Edwards *et al*., 1999
Bifurcating axis		*Velatitetas* sp.	Edwards *et al*., 1999
Irregular spore mass		? *Velatitetras rugulata*	Edwards *et al*., 2012b
Cooksonioid		*Acontotetras inconspicuis*	Edwards *et al*., 2012b
Paracooksonioid		*Acontotetras* sp.	Edwards *et al*., 2012b
Bifurcating axis		*Cheilotetras* sp.	Edwards *et al*., 1999
Valvate sporangium 1		*Cheilotetras* sp.	Edwards *et al*., 2012b
Valvate sporangium 2		*Cheilotetras* sp.	Edwards *et al*., 2012b
Irregular spore mass		*Cheiloteteas* sp.	Edwards *et al*., 2012b
Bifurcating axis		*Tetrahedraletes medinensis*	Edwards *et al*., 1999
Ovoid spore mass		*Tetrahedraletes medinensis*	Edwards *et al*., 1999
Irregular spore mass		*Tetrahedraletes* sp.	Edwards *et al*., 1999
Irregular spore mass		? *Tetrahedraletes* sp.	Edwards *et al*., 2012b
Alete monads			
Valvate sporangium		Sculptured alete monads	Edwards *et al*., 2012b
Incertae sedis			
cf. *Sporogonites*		Crassitate sculptured spores	Edwards, 1996

Figure 1. Relationships among major groups of land plants showing the hypothesized broad range of clades to which cryptophytes (cryptospore-producing plants) might belong (shaded oval). As currently envisaged, cryptophytes is a grade of organization potentially encompassing plants spanning the embryophyte to tracheophyte stem-groups as well as stem-group hornworts, mosses and liverworts. Some distinctive groupings are emerging, and here we recognise two (*Partitatheca*, *Lenticulatheca*), which we suggest occupy a comparatively derived position within polysporangiophytes. Relationships of living groups depicts one widely supported hypothesis based on: Charophytes (Timme *et al.*, 2012; Bowman, 2013); Liverworts (Heinrichs *et al.*, 2007); mosses (Cox *et al.*, 2010); hornworts (Shaw and Renzaglia, 2004; Villarreal et al., 2010); embryophytes (Qiu et al., 2007; Magallón et al., 2013); fossils (Kenrick & Crane, 1997). The broken lines joining *Partitatheca* and *Lenticulatheca* indicate that their phylogenetic positions are hypothesized. Polysporangiophytes is a clade containing living and extinct groups with branched sporophytes (Kenrick & Crane, 1997). Stomatophytes indicates a clade in which stomates are a synapomorphy but are inferred to have been subsequently lost in some extant taxa (Kenrick & Crane, 1997; Ligrone et al., 2012).


Euphyllophytes
Lycophytes
Eutracheophytes
Tracheophytes
Rhynia †
Cooksonia †
Polysporangiophytes
Lenticulatheca †
Aglaophyton †
Partitatheca †
Stomatophytes
Notothylas
Anthoceros
Hornworts
Takakiopsida
Sphagnopsida
Andreaeopsida
Peristomate mosses
Mosses
Embryophytes
Haplomitriopsida
Marchantiopsida
Jungermanniopsida
Liverworts
Coleochaetales
Zygnematales

within irregular spore mass. v) NMW98.23G.4; within irregular spore mass. (g) i) Ed

al., 1999. NMW96.11G.3; within basal sporangia terminating bifurcating axis. Lowe

Devonian. ii) Habgood, 2000. NMW99.19G.2, within elongate sporangium. Lower

Devonian. iii) Edwards *et al*., 2012b. V.68196(2); within irregular spore mass. Lowe

Devonian. iv) Taylor, 2000. Dispersed, Lower Silurian. v) Edwards *et al*., 1999.

NMW96.11G.4; within discoidal sporangium. Upper Silurian. (h) Edwards *et al*., 201

MNW2012.17G.1; within discoidal sporangium. Lower Devonian. (i) i) & ii) Edward

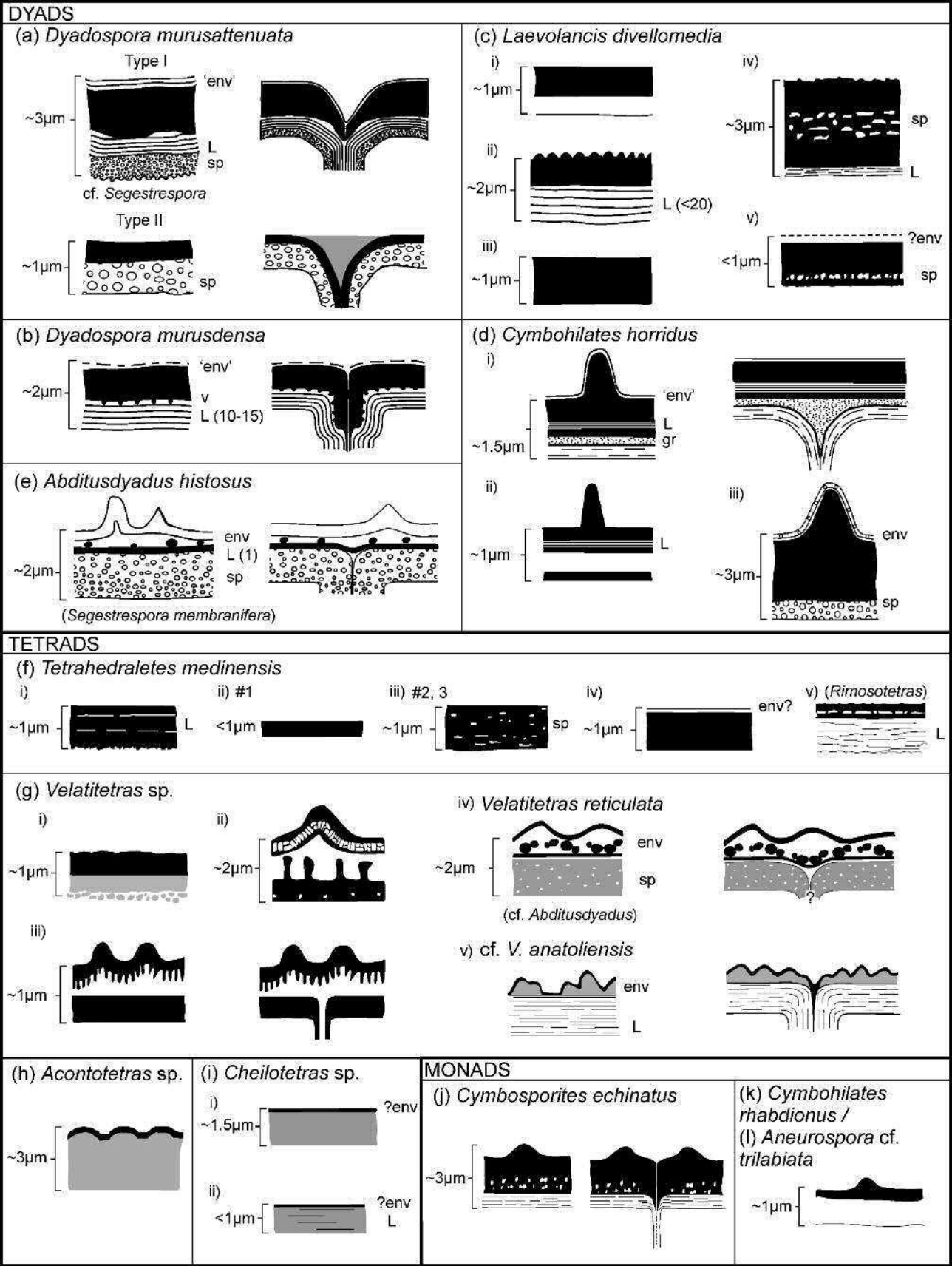
2012b. Lower Devonian. i) NMW2012.7G.3; within valvate sporangium. ii) NMW99

within ?valvate sporangium. (j) Johnson & Taylor, 2005.; dispersed. Upper Silurian.

Morris *et al*., 2011; Lower Devonian. (k) V.68188(1); within discoidal sporangium. (

V.68196(1); within discoidal sporangium. L, lamina; env, envelope; sp, spongy; gr, g

v, verrucae.


DYADS
(a) Dyadospora murusattenuata
Type I
~3µm
'env'
L
sp
cf. Segestrespora
Type II
~1µm
sp
(b) Dyadospora murusdensa
~2µm
'env'
v
L (10-15)
(e) Abditusdyadus histosus
~2µm
env
L (1)
sp
(Segestrespora membranifera)
(c) Laevolancis divellomedia
i)
~1µm
ii)
~2µm
L (<20)
iii)
~1µm
iv)
~3µm
sp
L
v)
<1µm
?env
sp
(d) Cymbohilates horridus
i)
~1.5µm
'env'
L
gr
ii)
~1µm
L
iii)
~3µm
env
sp
TETRADS
(f) Tetrahedraletes medinensis
i)
~1µm
L
ii) #1
<1µm
iii) #2, 3
~1µm
sp
iv)
~1µm
env?
v) (Rimosotetras)
L
(g) Velatitetras sp.
i)
~1µm
ii)
~2µm
iii)
~1µm
iv) Velatitetras reticulata
~2µm
env
sp
(cf. Abditusdyadus)
?
v) cf. V. anatoliensis
env
L
(h) Acontotetras sp.
~3µm
(i) Cheilotetras sp.
i)
~1.5µm
?env
ii)
<1µm
?env
L
MONADS
(j) Cymbosporites echinatus
~3µm
(k) Cymbohilates rhabdionus /
(l) Aneurospora cf. trilabiata
~1µm

(h) NMW99.19G.1; Habgood, 2000. (i) Bifurcating axis terminating with basal part

sporangium. (g) *In situ* spores; *Cymbohilates* cf. *horridus*. (h) TEM section through *C*

horridus. (i) - (k) *Partitatheca cymosa* Edwards *et al*., 2012a. V.68212(1) (holotype).

Whole specimen. (j) *In situ* spores; *Cymbohilates cymosus* Richardson, 1996a. (k) Dy

spinose elements arranged in star-shaped rosettes. (l) - (o) cf. *Partitatheca* sp. Morris

2012a. V.68264a(1) & V.68264b(1). (l) Whole specimen. (m) *In situ* spores; *Chelinol*

cf. *erraticus* (Richardson, 1996a). (n) Fractured section through dyad, with narrow int

wall. (o) LM of section through dyad, with narrow internal wall. (p) - (r) NMW97.42

Wellman *et al*., 1998a. (p) Whole specimen (single valve only). (q) *In situ* spores;

Dyadospora murusdensa Strother & Traverse emend. Burgess & Richardson, 1991. (r

section of *D. murusdensa*. Scale bars: (a), (i), (l), (p) = 200µm; (b), (g), (j), (m) - (o),

20µm; (c) = 10µm; (d) = 50µm; (e) = 1µm; (f) = 500µm; (h) = 2µm; (k) = 5µm; (r) =

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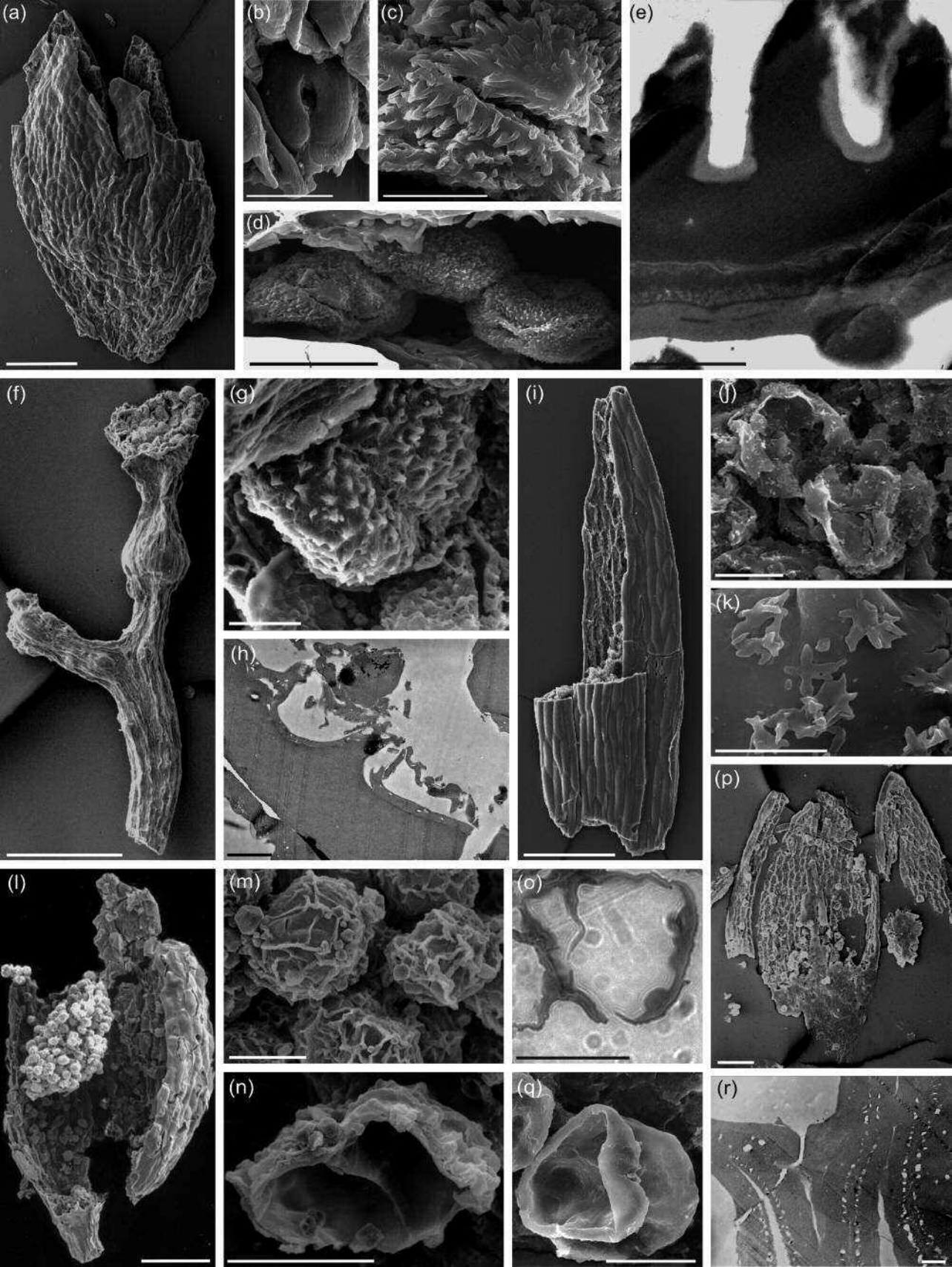
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NMW99.11G.2, Edwards *et al*., 2012. (c) Elongate bi-valved sporangium. (d) *In situ*

Cheilotetras sp. (g) TEM section through spore wall with laminate structure. (h) - (j)

NMW99.19G.2, Habgood, 2000. (h) Elongate bi-valved sporangium. (i) *In situ* spore

Velatitetras sp. (j) TEM section through spores; thick envelope with layer of voids, sp

wall homogeneous with outward projections. (k) - (m) *Culullitheca richardsonii* Wel

al., 1998a. NMW.96.11G.6. (k) Whole specimen. (l) *In situ* spores; *Dyadospora murt*

(m) TEM section through homogeneous spore wall. (n) - (p) *Fusiformitheca fanningi*

Wellman *et al*., 1998a; Xue & Wang, 2011. NMW97.42G.4. (n) Whole specimen. (o)

spores; enveloped, laevigate permanent dyads. (p) TEM section through homogeneou

wall. Scale bars: (a), (e) = 200µm; (b), (f), (i), (k), (l), (n), (o) = 20µm; (c) = 5µm; (d

(m), (p) = 1µm; (g) = 3µm; (h) = 500µm. Fig. 4(a-g) were first published in Edwards

2012b and are reproduced here with kind permission of Elsevier. Fig. 4(h-j) were firs

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4(k) was first published in Edwards, 1997 and is reproduced here with kind permissio

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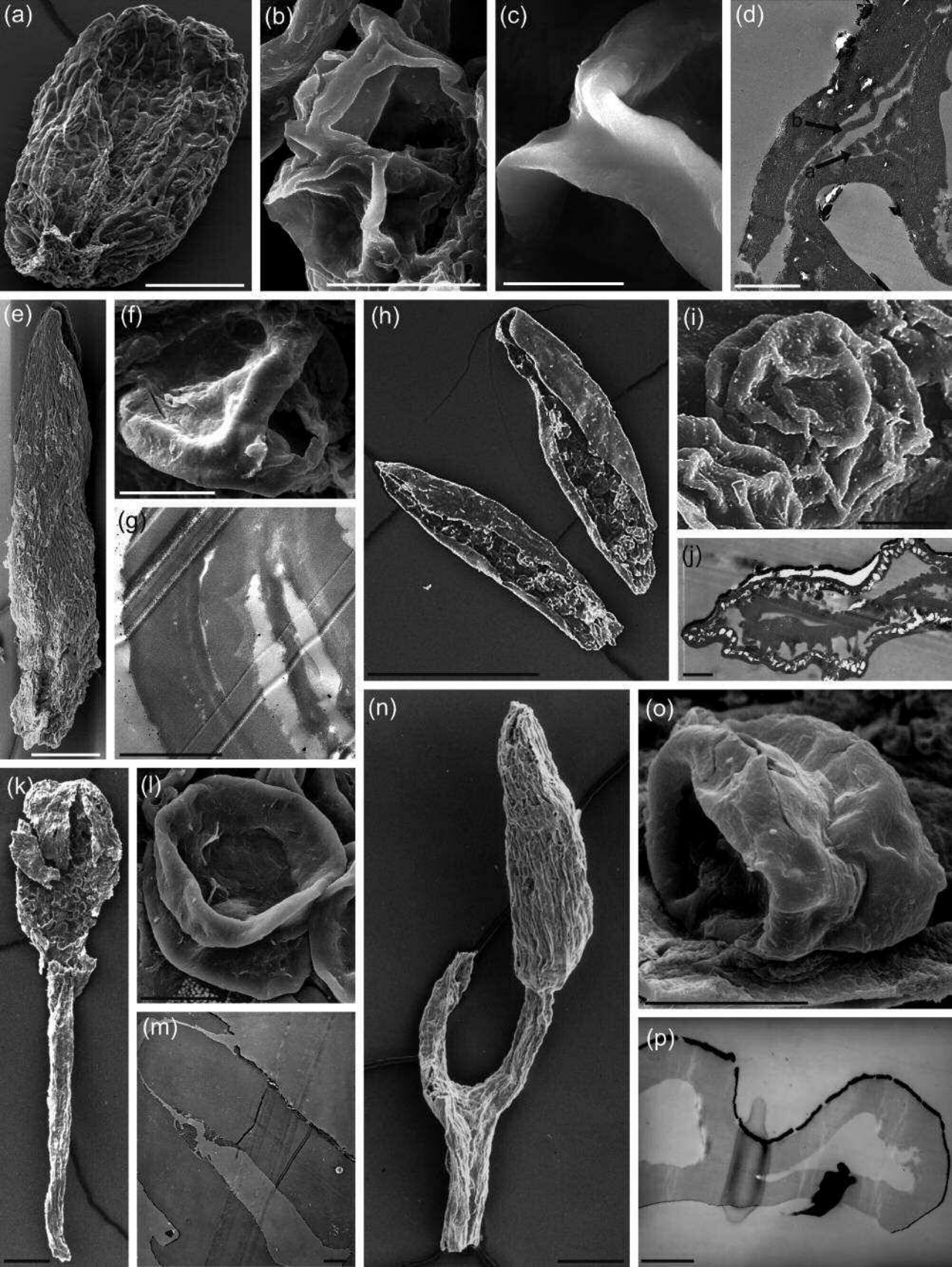
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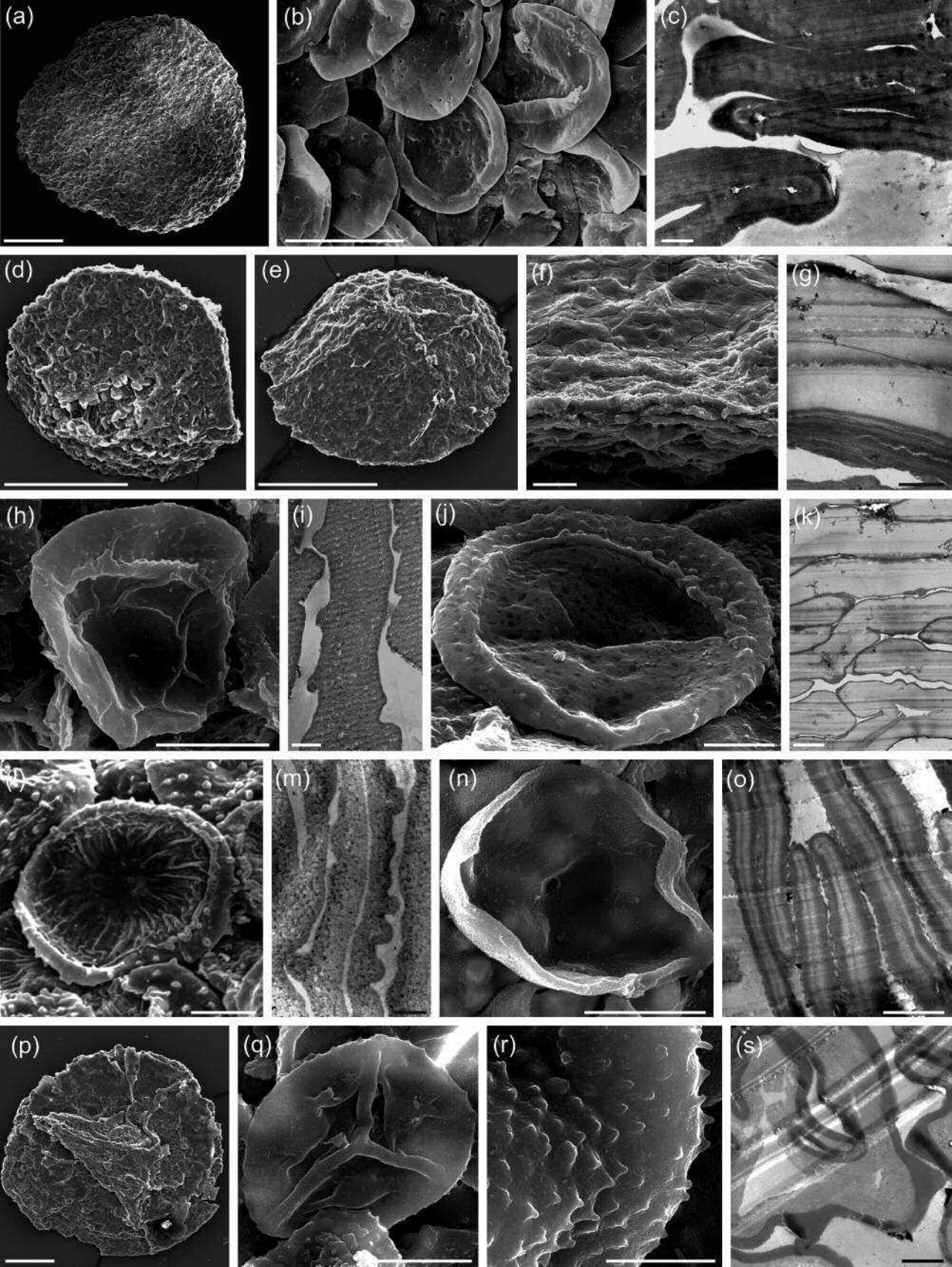
Specimen margin; spores occurring between two non-cellular layers. (g) TEM section through cuticle of *L. mesodeca*. (h) Spore within *L. magna*; *Cymbohilates allenii* var. Richardson, 1996a. (i) TEM section through *C. allenii* var. *magnus*. (j) Spore within *mesodeca*; *C. mesodecus* Richardson in Morris *et al*., 2011. (k) TEM section through *mesodecus*. (l) Spores within *L. variabilis*; *Cymbohilates variabilis* Richardson, 1996 TEM section through *C. variabilis*. (n) Spore within *L. allenii*; *Cymbohilates allenii* v *allenii* Richardson, 1996a. (o) TEM section through *C. allenii* var. *allenii*. (p) – (s) *Paracooksonia apiculispora* Morris *et al*., 2011. (p) - (r) V.68189(1) (holotype). (p) V specimen. (q) – (r) *In situ* spores; *Streelispora newportensis* Richardson & Lister 196 Proximal surface; (r) Distal surface. (s) TEM section through *S. newportensis*. V.681 Scale bars: (a), (d), (e), (p) = 200µm; (b), (f) = 20µm; (h), (l), (n), (q) = 10µm; (j), (r) (k) = 3µm; (c), (g), (i), (m), (s) = 1µm; (o) = 2µm. Fig. 5(a), (c) were first published i Wellman *et al*., 1998b and are reproduced here with kind permission of The Royal So Fig. 5(b) was first published in Edwards *et al*., 1998 and is reproduced here with kind permission of Maney. Fig. 5(d) - (s) were first published in Morris *et al*., 2011 and ar reproduced here with kind permission of Elsevier.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members of a tetrad, with thick distal walls (D) and thin, unfused proximal walls (P).

NMW2012.17G.1 Edwards *et al*., 2012b. Discoidal sporangium containing permanen

sculptured tetrads. (e) Whole specimen, with stomata (arrow). (f) Cross section throu

sporangial wall composed of rectangular cells. (g) – (j) *In situ* spores; *Acontotetras*

inconspicuis Richardson, 1996a. (g) Tetrad with major ridges and invaginations. (h) F

tetrad with slight furrow (arrow). (i) Tetrad with ridges, sculptured with micrograna t

biform elements. (j) Variation in sculptural elements between adjacent tetrads. (k) TE

through tetrad, with thick distal walls and thin proximal walls. (l) LM of thin section

tetrads, with thick distal walls and thin envelope surrounding entire tetrad, with sinuo

(arrows a & b) representing the junction between tetrad members. Proximal walls are

extend into the lumen (arrow c). (m) – (r) NMW2012.17G.5 Edwards *et al*., 2012b.

Sporangial fragment containing alete monads. (m) Whole specimen. (n) Sporangial w

elongate cells. (o) Alete monad with major ridges and invaginations, sculptured with

spaced coni, microconi and micrograna. (p) Ridge of tetrad with slight furrow. (q) LM

section through two alete monads, fused together by sculptural elements (arrow). (r) I

thin section through two alete monads, fused together by sculptural elements, with an

additional thin layer occurring between (arrow). Scale bars: (a), (e), (n) = 200µm; (b),

(o), (p) = 20µm; (c), (d), (h), (i), (j), (l), (q), (r) = 10µm; (k) = 5µm; (m) = 500µm. Fig

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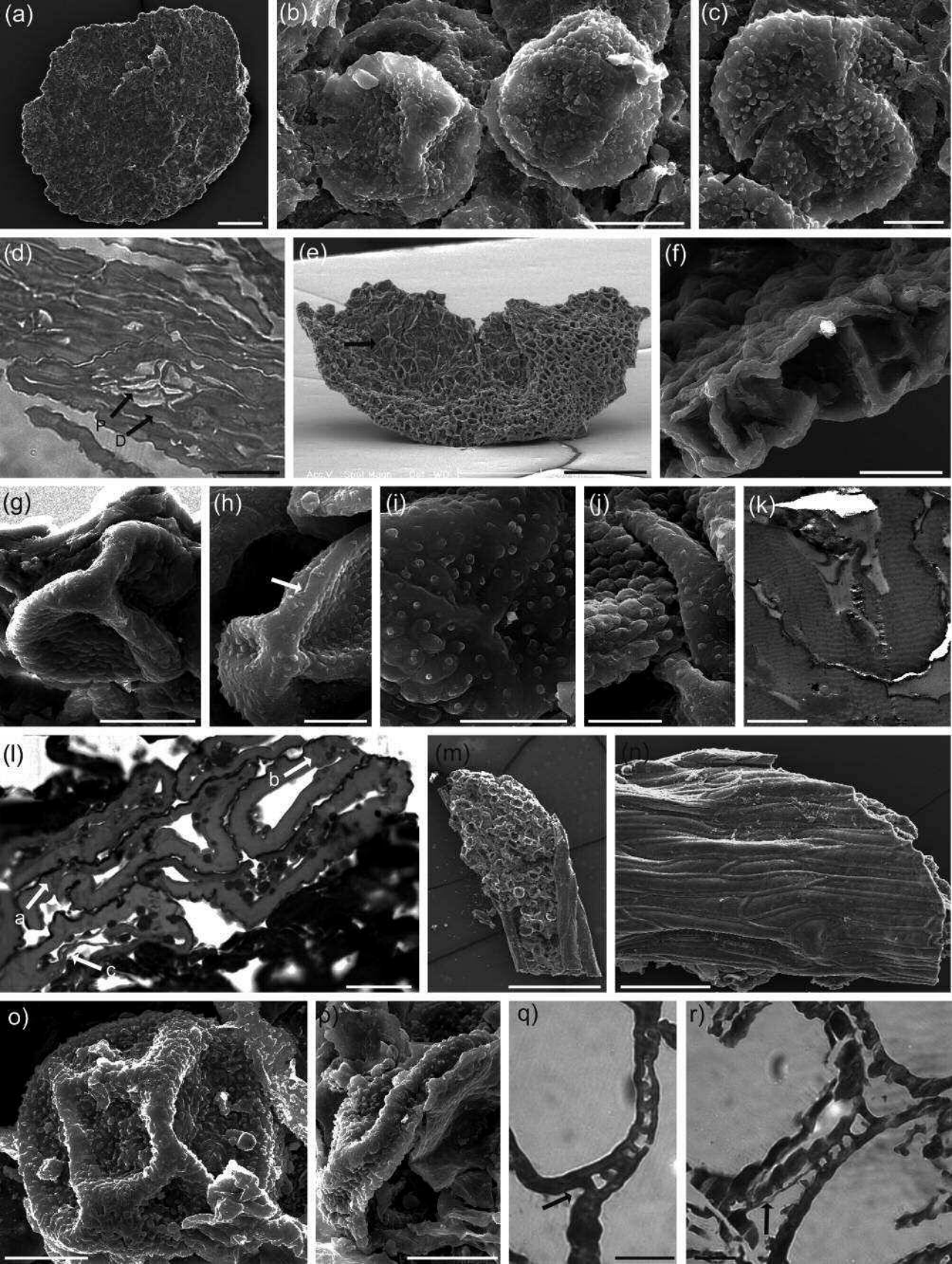
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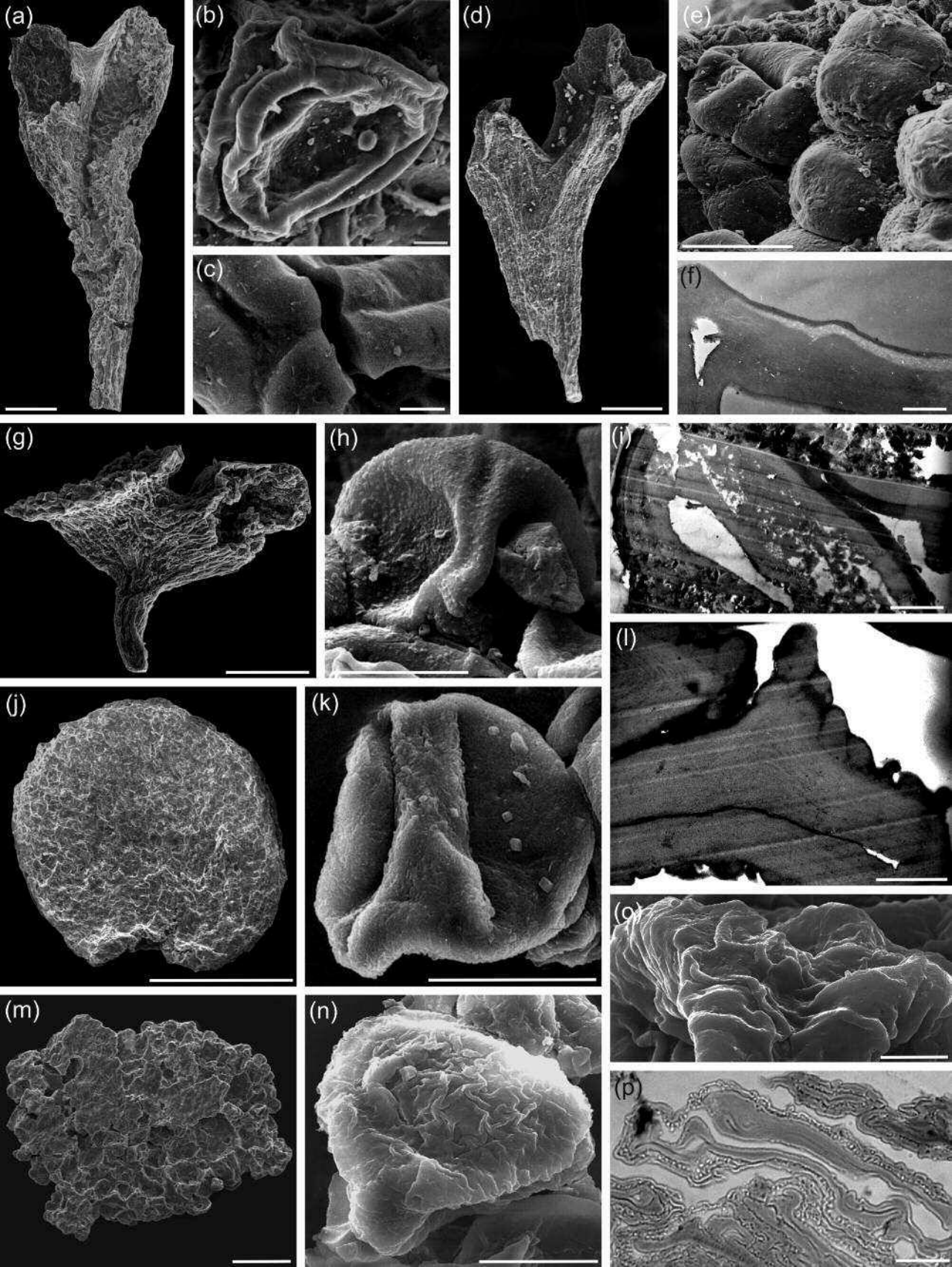
spores. *Retiacolpites meadensis*. (f) TEM section of *in situ* spores, note separating layer. (g) – (i) NMW96.11G.3. Edwards *et al*., 1999. (g) Bifurcating axis terminated b bases of two sporangia. (h) *In situ* spore: *Velatitetras* sp. (i) TEM section through *in s* spores; note the tri-layered wall, with a central zone of globular material. (j) – (l) NMW96.11G.4. Edwards *et al*., 1999. (j) Discoidal spore mass covered with amorpho layer. (k) *In situ* spore: *Velatitetras* cf. *anatoliensis*. (l) TEM section through *in situ* sp note tightly adherent envelope and faint striations in the inner wall. (m) – (p) V.68196 Edwards *et al*., 2012b. (m) Irregular shaped spore mass covered with cuticular layer. *situ* spores: *Velatitetras* sp. (o) Magnification of tetrad surface, enclosed within envel superficial sinuous folding. (p) LM of thin section through tetrad, illustrating a thick 'envelope' with inward projections separate from the internal spore. Scale bars: (a), (n 200µm; (b), (o) = 5µm; (c) = 2µm; (d), (j) = 500µm; (e), (j) = 50µm; (f) = 500nm; (g) 100µm; (h), (p) = 10µm; (i), (l) = 1µm; (k), (n) = 20µm. Fig. 7(a), (b) were first publi Edwards *et al*., 1995b and are reproduced here with kind permission of Nature Publis Group. Fig. 7(c) - (f), (i), (k), (l) were first published in Edwards *et al*., 1999 and are reproduced here with kind permission of Wiley. Fig. 7(g), (h), (j) were first published Edwards, 1997 and are reproduced here with kind permission of Springer Science+Bu Media. Fig. 7(m) - (p) were first published in Edwards *et al*., 2012b and are reproduce with kind permission of Elsevier.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fused proximal walls (arrow a) and triangular thickenings where the distal walls are fu
together (arrow b). (f) LM of thin section through tetrad, showing four units of a tetra
free proximal walls and either partial (arrow a) or complete (arrow b) lines of attachm
between units. (g) – (n) *Ficoiditheca aenigma* Morris *et al*., 2012a. (g), (i), (m) V.682
(holotype). (g) Whole specimen. (h) V.68225a(1). Partial apical dehiscence via triang
tipped valves. (i) Section through proximal part of sporangial wall of holotype; irregu
to inside. (j) V.68228(1). Partially complete inflated spherical spores with microgranu
outer surfaces. (k) V.68258(1). Magnification of a spore surface, covered with a clust
microgranules, composed of smaller spheres. (l) V.68226a(1). ? dyad with invaginate
and two sub-equatorial concentric folds, separated by a central furrow. (m) TEM of tr
layered spore wall in holotype. Middle electron-dense layer thickens into a wedge wh
two units of a dyad meet to form an internal wall. (n) V.68259(1). TEM section throu
layered spore wall. (o) – (r) NMW96.11G.2, Wellman *et al*., 1998b. (o) Elongate
sporangium. (p) *In situ* spores: *Laevolancis divellomedia*. (q) & (r) TEM sections thro
spores; layered walls bearing granules across the outer surfaces. Scale bars: (a), (o) =
(b), (c), (d), (j), (p) = 20µm; (e), (f), (i) = 10µm; (g), (h) = 100µm; (k), (m), (n), (q), (
1µm; (l) = 5µm. Fig. 8(a) - (f) were first published in Edwards *et al*., 2012b and are
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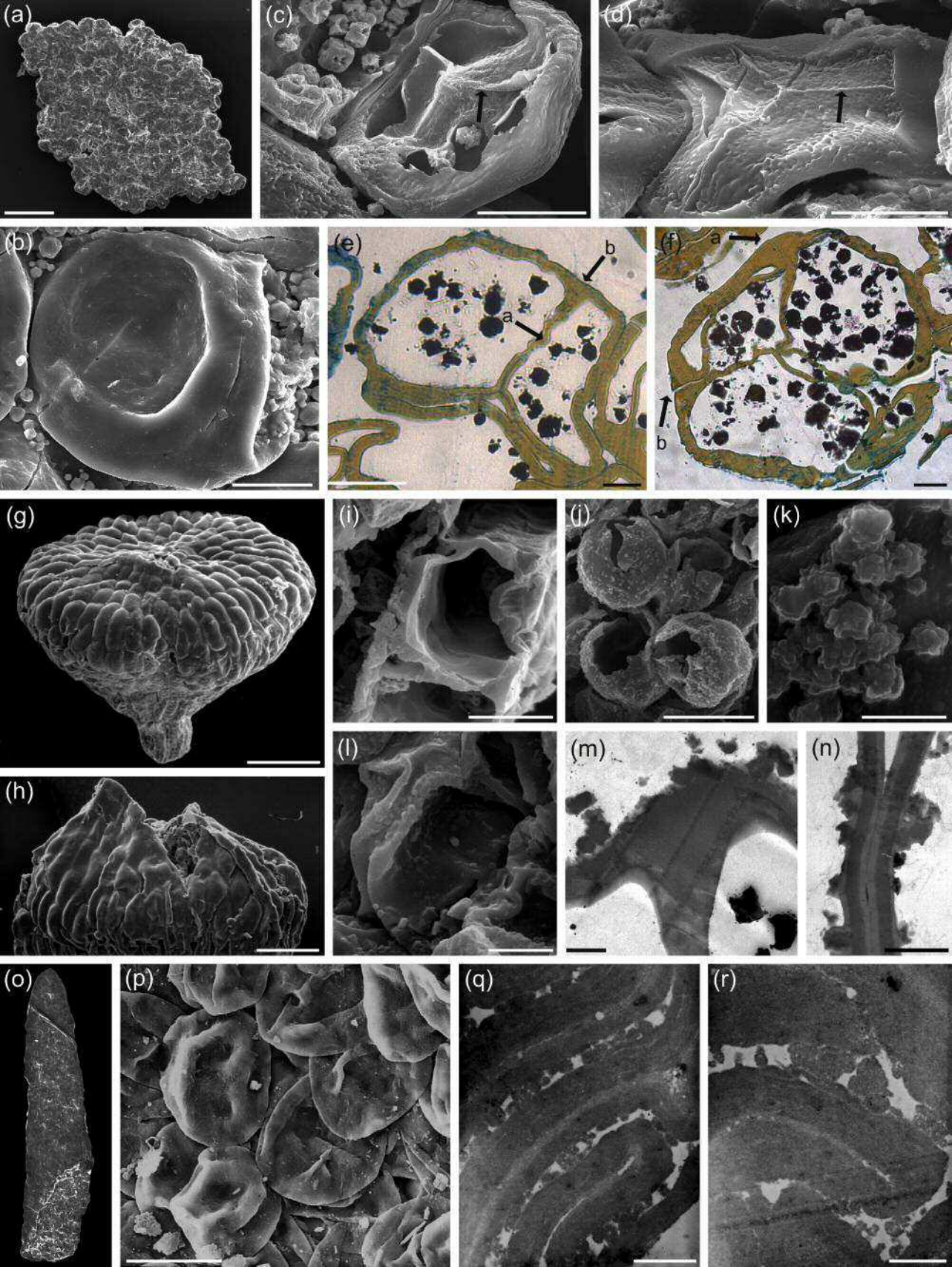
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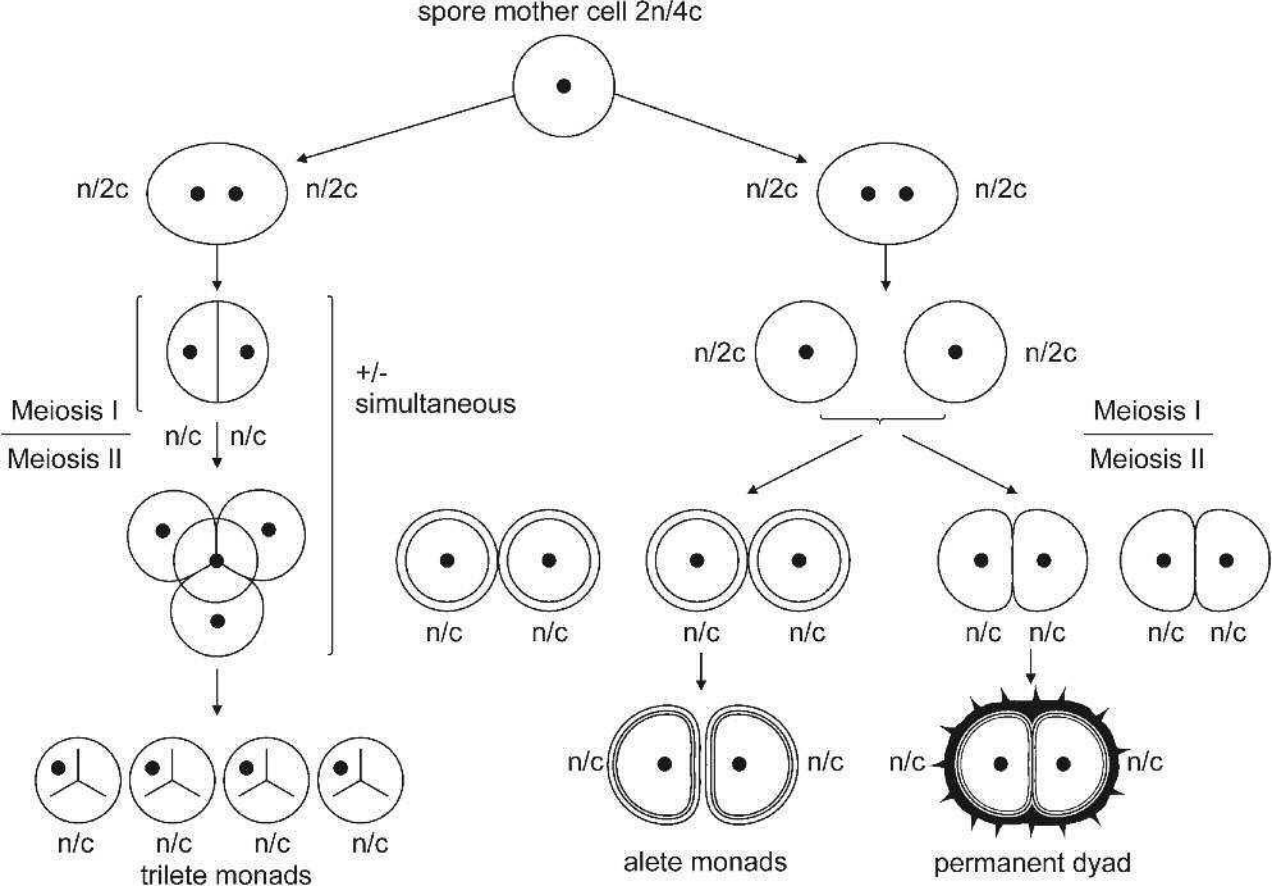
Devonian
Silurian
Ordovician
Frasnian
Middle
Givetian
Eifelian
Lower
Emsian
Pragian
Lochkovian
Přídolí
Ludlow
Ludfordian
Gorstian
Wenlock
Homerian
Sheinwoodian
Llandovery
Telychian
Aeronian
Rhuddanian
('Ashgill')
Hirnantian
Upper
Katian
('Caradoc')
Sandbian
('Llanvirn')
Middle
Darriwilian
('Arenig')
Dapingian
Cheilotetras caledonica
Rimosotetras problematica
Tetrahedraletes medinensis
Acontotetras inconspicius
Velatitetras laevigata
Velatitetras reticulata
Velatitetras cristata
Velatitetras anatoliensis
Velatitetras retimembrana
Dyadospora murusattenuata
Dyadospora murusdensa
Cymbohilates cymosus
Cymbohilates horridus
Cheilinohilates erraticus
Abditusdyadus laevigata
Segestrespora laevigata
Abditusdyadus histosus
Segestrespora membranifera
Segestrespora rugosa
Laevolancis divellomedia
Laevolancis plicata
Cymbohilates allenii var. allenii
Cymbohilates allenii var. magnus
Cymbohilates disponerus
Cymbohilates variabilis
Cymbohilates variabilis var. variabilis
Cymbohilates variabilis var. parvidecus
Imperfectotrietes vavrdovae
Ambitisporites avitus
Ambitisporites dilutus
Synorisporites verrucatus
Morphon
Streelispora -Aneurospora-Leonispora*
Cymbosporites echinatus
L
S
L
S
Naked
Enveloped
Permanent tetrads
L
S
L
S
Naked
Enveloped
Permanent dyads
L
S
Naked
Hilate monads
L
S
Naked
Trilete monads
Key
L = Laevigate
S = Sculptured
Dark red line = Anglo-Welsh Basin
Dark blue line = Global
Light blue/red = possible range
= questionable occurrences
= suspected reworking


spore mother cell 2n/4c
n/2c
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Meiosis I
Meiosis II
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+/-
simultaneous
Meiosis I
Meiosis II
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trilete monads
alete monads
permanent dyad